SPAWNING DISTRIBUTION OF ATLANTIC SALMON (*Salmo salar* L.) IN CONTROLLED FLOW CHANNELS

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by

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ABSTRACT

The spawning distribution of Atlantic salmon in specially designed controlled flow channels was studied in relation to spawning density, water temperature, water velocity, water depth, test egg plant mounds, rock weirs, and floating shelters in an attempt to devise management procedures which would reduce egg mortality on the spawning beds arising from egg nest overlap and egg predation.

Behavior observations included daily counts of spawners occupying beds in various sections, daily positioning of tagged fish in some sections and continuous surveillance of pairs spawning in the channels or in a specially built observation chamber. Spawning area placed into egg nests was plotted daily and the patterns of redd locations were examined by comparison to theoretical probability distributions. Test egg plant mounds, weirs and shelters were installed in the channel and current patterns noted about the former two. Daily water temperature fluctuations and daily fluctuations in fish frequenting spawning beds were correlated.

Adults spawned successfully free of serious predation, disease or egg retention. Territorialism and mating were observed in established pairs. The territory often changed in locale and mate especially amongst the males. Females did not always place their spawnings in one redd and one redd was often composed of eggs from several different females. Resident salmon parr and trout were discovered as potential salmon egg predators. Analysis indicated randomness in the redd patterns but contagion was isolated on one channel section containing a rock weir. As the spawning density was raised in channel sections, the redd area diminished but redd

superimposition still continued to increase. At the highest spawning density imposed of 1 female per 6.4 square yards 25 per cent of the bed area was in redds with 13 per cent of this superimposed. The correlation of daily water temperature fluctuations with spawning activity was significant in one year but insignificant the following year. Salmon were flexible in their water velocity and water depth preferences at redd sites and selections were largely a reflection of the water profiles available. The test egg plant mounds affected the redd distribution; current patterns about the mounds indicated an area of maximum subterranean current on the forward slope of the mounds where adults placed redds. Spawners congregated notably under shelter in holding pools but not under shelter over spawning bed.

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I. INTRODUCTION

Distribution of adult fish during spawning has long been regarded as important to the survival of members of the family Salmonidae which place their eggs in gravel beds of streams. This has especially received attention in Pacific salmon species where high spawning densities often result in an overlap in egg nests and redds built, increased egg predation, and mortality accompanying these effects (Gilbert and Rich, 1927; McNeil, 1964). However, territorial behavior in salmonids as with other animals has tended to reduce these damaging effects since it has spaced the adults and their nests (Tinbergen, 1952; Fabricius and Gustafson, 1954). Research has ensued into these opposing factors to determine what spawning densities should prevail for effective management of the spawning populations or escapements.

In the case of the Atlantic salmon (Salmo salar) which inhabit Atlantic coast streams, the mortality factors mentioned above are probably not as critical. Here, the spawning populations or spawning escapements tend to be much smaller than in Pacific coast streams meaning that the demand for spawning space and the incidence of egg mortality are generally less. Nonetheless, on the Island of Newfoundland, there is research being carried out to determine the feasibility of placing large numbers of spawners into channels with controlled spawning and egg incubation conditions as part of an effort to maintain or develop salmon runs in streams. Hence, the role which spawning density and channel design play in distribution of Atlantic salmon is quite important and should be explored.

This is the first time that a channel facility of this kind has been used in the spawning management of the Atlantic salmon. The writer

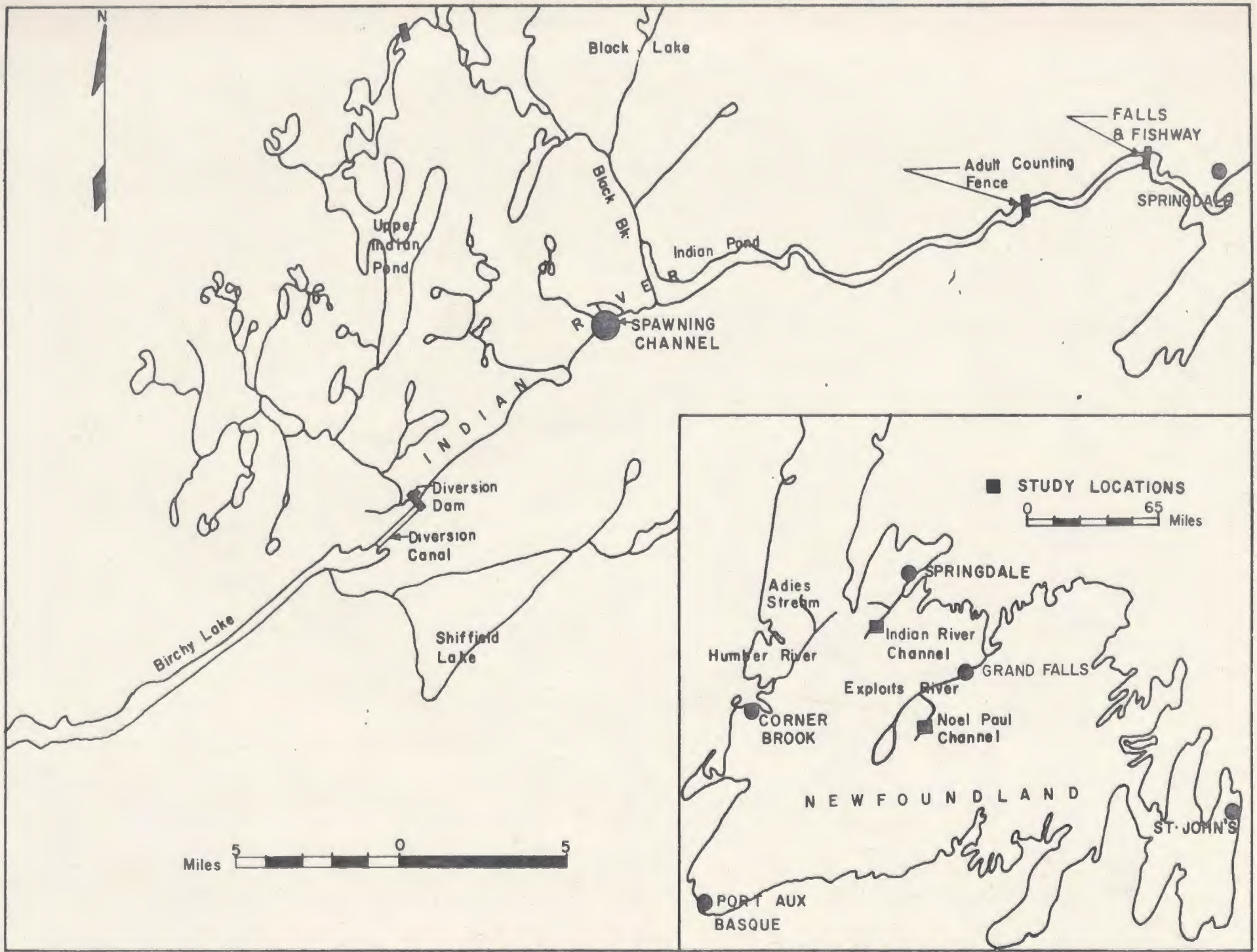


Fig. 1. Map of Indian River watershed with inset of Newfoundland showing study locations.

Fig. 2. View of Indian River Controlled Flow Spawning Channel with test pen shown.

Fig. 3. View of Noel Paul's Controlled Flow Spawning Channel with observation chamber shown.

has, therefore, also reported on a few points about salmon spawning in channels which are not that pertinent to the topic but may still interest persons studying salmonids.

Indian River Controlled Flow Channel and Noel Paul's Controlled Flow Channel are two channels which have now been placed into operation in Newfoundland. In both cases, the channel design is quite similar, with the longitudinal axis running roughly parallel to the particular adjacent stream. One or two water intake valves control the water through them from the stream while the gradient and width design provide velocities and depths of water within them at a regime similar to that previously measured on utilized spawning beds of Newfoundland salmon streams. The general dimensions and hydraulic conditions provided by each channel's design during the study are given in Table I. Spawning areas with holding pools separating them constitute each channel. Each area contains stream gravel screened with machinery to the specifications shown in Fig. 4.

Channel environments such as those described above afford many advantages for conducting studies of spawning distribution because observations are done under semi-wild conditions. Because of controlled flow and environmental uniformities created in the hydraulics and bottom type by design, the result is a compromise between the artificial aquarium or tank situation and the natural river spawning environment. Jones (1959), in his studies of spawning Atlantic salmon found field observations of fish under natural conditions extremely difficult to make and interpret. However, by use of tanks, artificial light and slow motion cinephotography, Jones and King (1949, 1950) were able to make continuous and thorough observation of salmon behavior mainly at the intra-pair level.

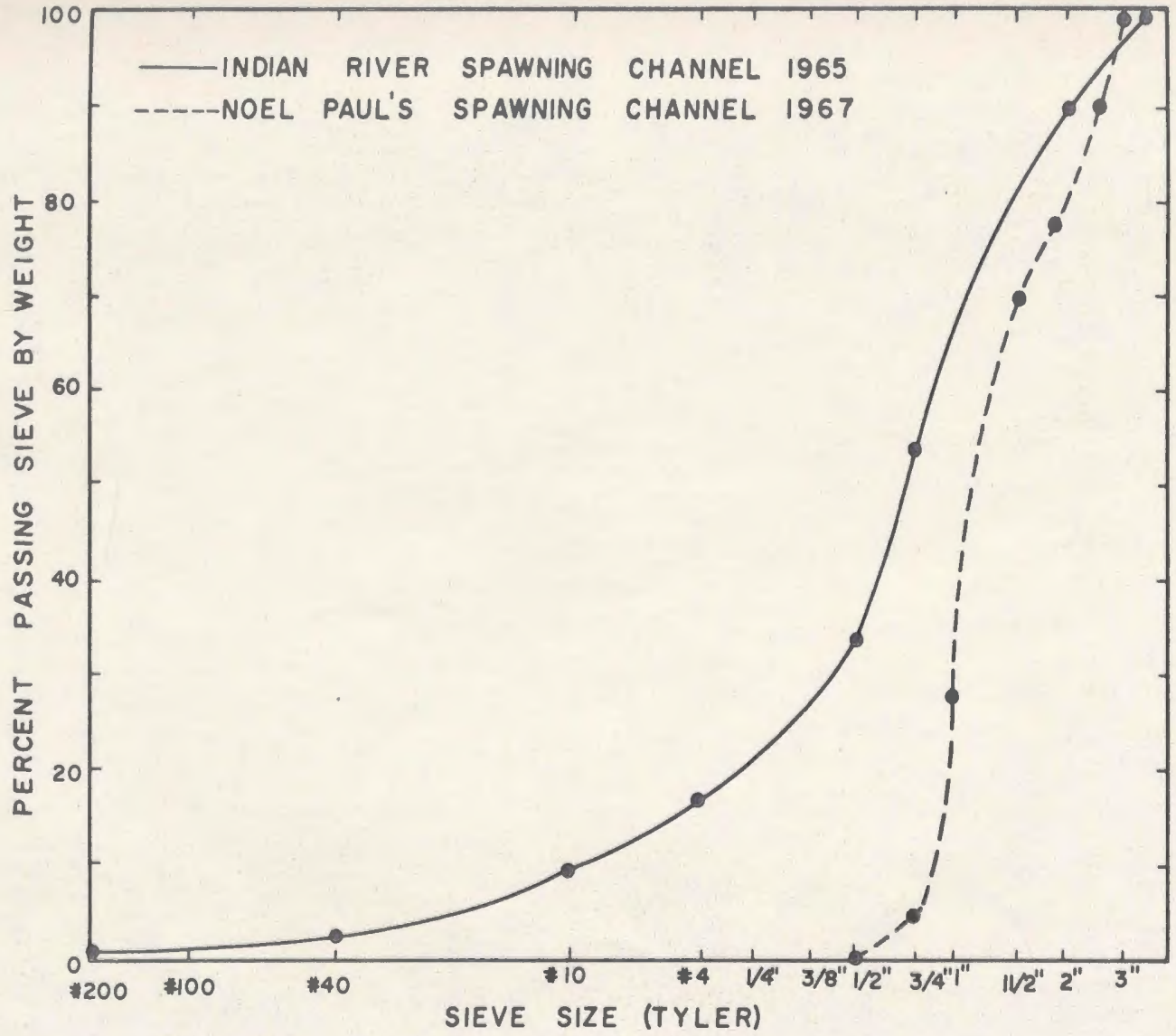


Fig. 4. Grading curves for gravel from spawning beds, Indian River and Noel Paul's Controlled Flow Channels, 1965, 1967.

Table I. Dimensions and hydraulic conditions used at Indian River and Noel Paul's Channel during study.

Factor	Indian River	Noel Paul's Brook
Length in feet (approximate)	1130	900
Width during study	16	16
Discharge in cubic feet per second during study	18	15
Bed water velocity (feet per second)	0.5 - 2.5	0.5 - 2.5
Bed water depths (feet)	0.5 - 2.0	0.5 - 2.0
Holding pool depths (feet)	2.5 - 5.0	2.5 - 4.0

The facilities provided by Indian River Channel would not allow this detailed level of study, but they did provide for extension of spawning studies to include more of the relationships between various spawners in an environment more controlled than a natural river spawning ground. Single pairs of spawners were confined to small areas of channel (i.e. "test pens") for intra-pair study, but most of the emphasis was placed on examining the spawning of fish held in larger numbers in larger areas or "sections" where the spawning densities could be manipulated. Noel Paul's Channel, which handled its first spawning population in 1967, also managed to provide some added information on spawning and distribution before this study was completed. Here, a spawning observation chamber similar in principle to that described by Jones (1959) and Lindroth (1954) is being used. More important, a group of spawners confined to one

spawning area greatly substantiated certain results collected on distribution at Indian River during 1965 and 1966.

The physical aspects of water temperature, light, precipitation, water velocity, water depth, subsurface seepage, weirs and shelters were surveyed and their relationship to the spawning distribution assessed. The effect of fluctuations in water temperature and light on day to day spawning has been noted in other species of salmonids (Fabricius, 1954; Fabricius and Gustafson, 1955). The significance of water current and water depth to adult distribution has been established and these factors have received intensive examination on both natural and artificial spawning grounds (Chambers, et al, 1955; Fouraton and Mackinnon, 1956). It has also been observed that some salmonids spawn at places where there is seepage through the bottom material (White, 1930; Greeley, 1932; Hazzard, 1932; Needham and Taft, 1934; Stuart, 1953; 1954). The possibility of such seepage about egg plants and weirs placed in the spawning bed of a channel was examined in light of the spawning distribution which prevailed. The connection of man-made shelter to the distribution of spawning and resting adults was also investigated.

The distribution study at Indian River Channel was conducted mainly with spawners from the 1965 and 1966 river populations although some information collected with the 1963 and 1964 populations was also included. A summary of length, weight and sex ratio for the 1965 and 1966 spawning escapements is presented in Table II. The supplemental information collected from Noel Paul's Brook Channel in 1967 involved about 25 fish which were collected and transferred from Adies Stream, a tributary of the Upper Humber River in Newfoundland (Fig. 1). Their size and sex

features are also given in Table II. The age composition for the three seasons was mainly composed of adults in their fifth or sixth year, few of which had previously spawned or spent more than one year at sea. Atlantic salmon possessing this type of life cycle are usually referred to as "grilse" (Jones, 1959).

Table II. Sex, length and weight of spawning escapements, Indian River Spawning Channel, 1965, 1966, Noel Paul's Channel, 1967.

	Year	No. in channel	Sex Ratio		Average length (cm)		Average weight (lbs)	
			Female	Male	Female	Male	Female	Male
Grilse	1965	140	77	23	50.0	50.0	3.2	2.8
Salmon		2	100	0	73.0	-	8.0	-
Grilse	1966	144	78	22	48.0	49.0	2.9	2.6
Salmon		2	100	0	66.0	-	6.6	-
Grilse	1967	25	55	45	53.7	55.7	3.2	3.3

The first part of this study discusses spawning behavior and spawning density in relation to adult distribution. The second part deals more with physical aspects of the channel environment and how they affect the distributions. Finally, the third part discusses the importance the findings have to management of Atlantic salmon spawning populations in both channel and river environments.

II. METHODS AND MATERIALS

A. Biological Aspects of Spawning Distribution

1. Spawning Behavior

Studies were carried out to gain information on particular aspects of spawning behavior both at Indian River and Noel Paul's Channel. For the observation of courting, territorial defense, and actual spawning, both unmarked fish and fish marked with large coloured Petersen baffles were studied on the channel spawning beds. Marking was carried out several days before spawning commenced in order to allow fish to condition to the tags. Isolated pairs were also observed in test pens or observation chambers (for particulars on separations, see following section on Spawning Density).

At Indian River, reactions of channel pairs actively defending a spawning territory from encroachments by intruders were observed on Section III during 1966. These reactions were recorded according to type, frequency, level of intensity and sex of the tenants involved. For each approach of an intruder to the pair, a reaction was recorded for each member of the pair. A wire grid composed of eight foot squares was installed in the channel along with stakes placed at two foot intervals beside the channel. This facilitated the locating of spawners. To ensure rapid but accurate observations, a portable tape recorder was used to record a partially coded format of reactions devised from casual spawning observations conducted during previous spawning seasons (Pratt, 1964; Pratt and Sturge, 1965):

First Level

1 (a) Reactions terminated by retreat of intruder without apparent threat display.

1 (b) Reactions terminated by retreat of resident without apparent threat display.

Second Level

2 (a) Contacts terminated by retreat of intruder after mild to moderate one-sided threat display by resident. Shouldering and/or drifting movement frequent.

2 (b) Contacts terminated by retreat of resident after mild to moderate one-sided threat display by intruder. Shouldering and/or drifting movement frequent.

Third Level

3 (a) Contacts terminated by retreat of intruder after intense one-sided active attack by resident; darts with frequent snapping and occasional biting.

3 (b) Contacts terminated by retreat of resident after intense one-sided active attack by intruder; darts with frequent snapping and occasional biting.

Fourth Level

4 (a) Contacts terminated by retreat of intruder after moderate to intense reciprocal aggression; snapping and biting frequent.

4 (b) Contacts terminated by retreat of resident after moderate to intense reciprocal aggression; snapping and biting frequent.

For a study of the territory of spawning Atlantic salmon, the term "spawning territory" corresponded to Noble's (1939) definition of territory namely, "any defended area". Only paired males and females were observed for reactions to outsiders.

At both channels, daily counts of fish observed on the spawning areas were also recorded four times daily: daybreak (0730 hrs), afternoon (1600-1700 hrs), evening (2000 hrs), and midnight. To complete the evening and midnight census, it was necessary to "spot" fish in the light beam of a battery lantern. Tagged specimens were identified and their positions recorded.

2. Spawning Density

In order to assess the relation of fish density to spawning distribution in the channels, spawners were placed in several lots at different densities.

In 1955, the Indian River spawning escapement was divided into three parts by placing screen barriers or fences at particular points across the channel. These fish impoundments were called spawning sections and assigned a number (Fig. 5). In Section I (upper part of Spawning Area One) a spawning pair was introduced into each of two "test pens". In the upper pen (Pen A), a raiseable floor was placed under the spawning bed gravel. Following the spawning season, the floor was elevated to facilitate detailed plotting of any egg nests placed in the bed by the pair. Twenty-one fish were Petersen tagged with large coloured baffles and confined to Section II, which occupied the remaining space of Spawning Area One to Pool One. Downstream, Section III contained 121 fish which occupied the rest of the channel.

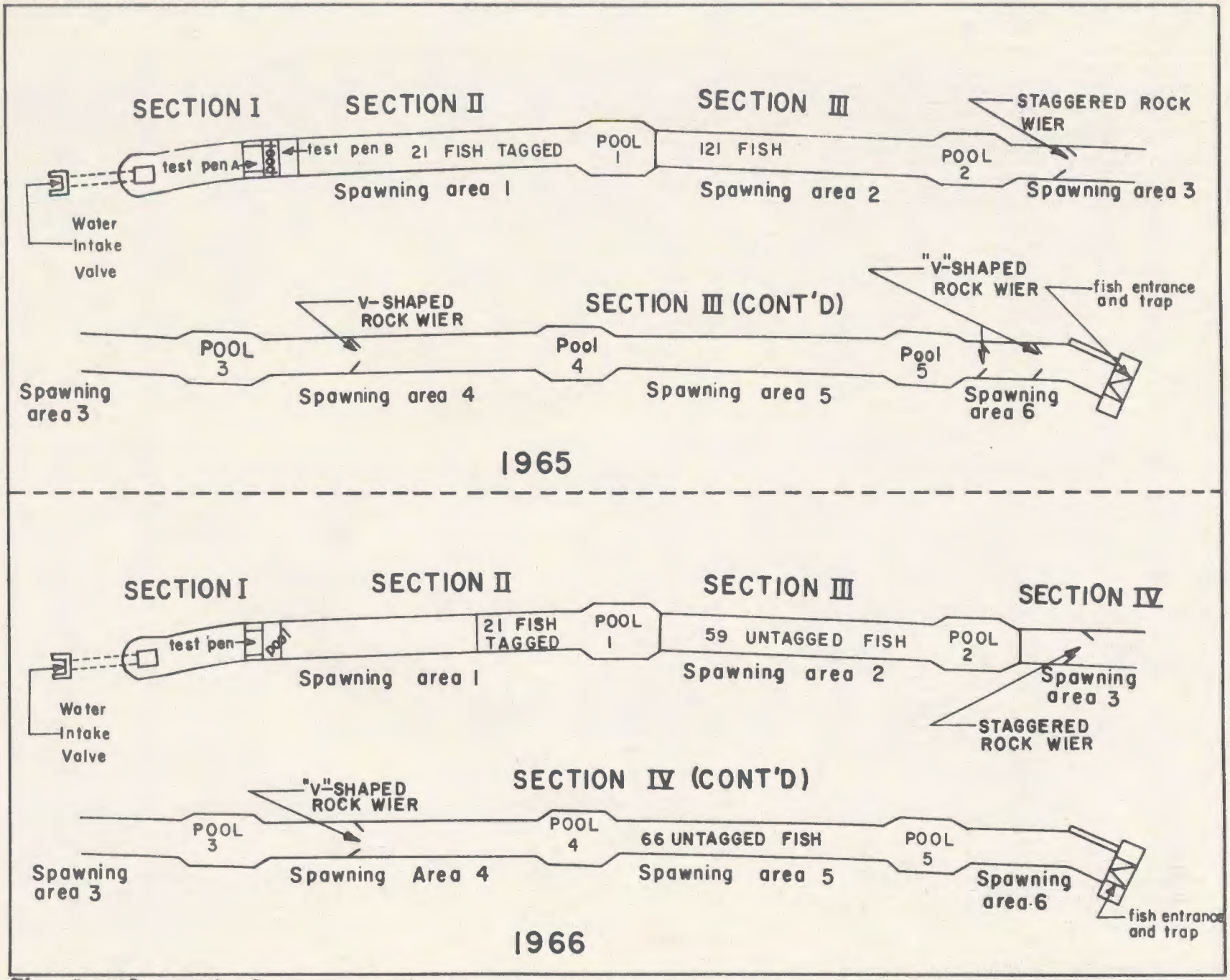


Fig. 5. Placement of spawners and rock weirs in channel by section, spawning area and year, Indian River, 1965, 1966.

In 1966, the escapement, at Indian River, was separated into four sections. In the first section, only one test pen, with one spawning pair, was maintained (Fig. 5). Twenty-one fish were again tagged and isolated in Section II but in less space than in 1965 and hence at higher density. Section III contained 59 fish and occupied Spawning Area Two at the same density as the tagged fish in Section II. Section IV, with 66 fish, included Spawning Areas Three, Four, Five and Six.

In 1967, one tagged male and two tagged females were placed in the Noel Paul's observation chamber for study of spawning detail. In Noel Paul's Channel, 25 spawners were marked and placed in Section A (Fig. 6).

In all years of observation, separation was carried out several days before spawning commenced in order to allow fish to condition to their new sections. The populations were also placed in the sections at the same sex ratio as that prevailing for the entire channel population at the time.

Table III summarizes the density separations made with the 1965, 1966, and 1967 escapements. In the fifth column, a density index which takes the untagged portion of the 1965 escapement as unity indicates the comparative densities for all separations.

Redds as they commenced were plotted daily onto plan view maps for a study of redd distribution. Their areas were outlined on engineering grid paper and measured with a planimeter. Accurate plotting of redds required staking the channel bank at two foot intervals and the use of a machine designed for drawing and orienting them within the channel (Fig. 8).

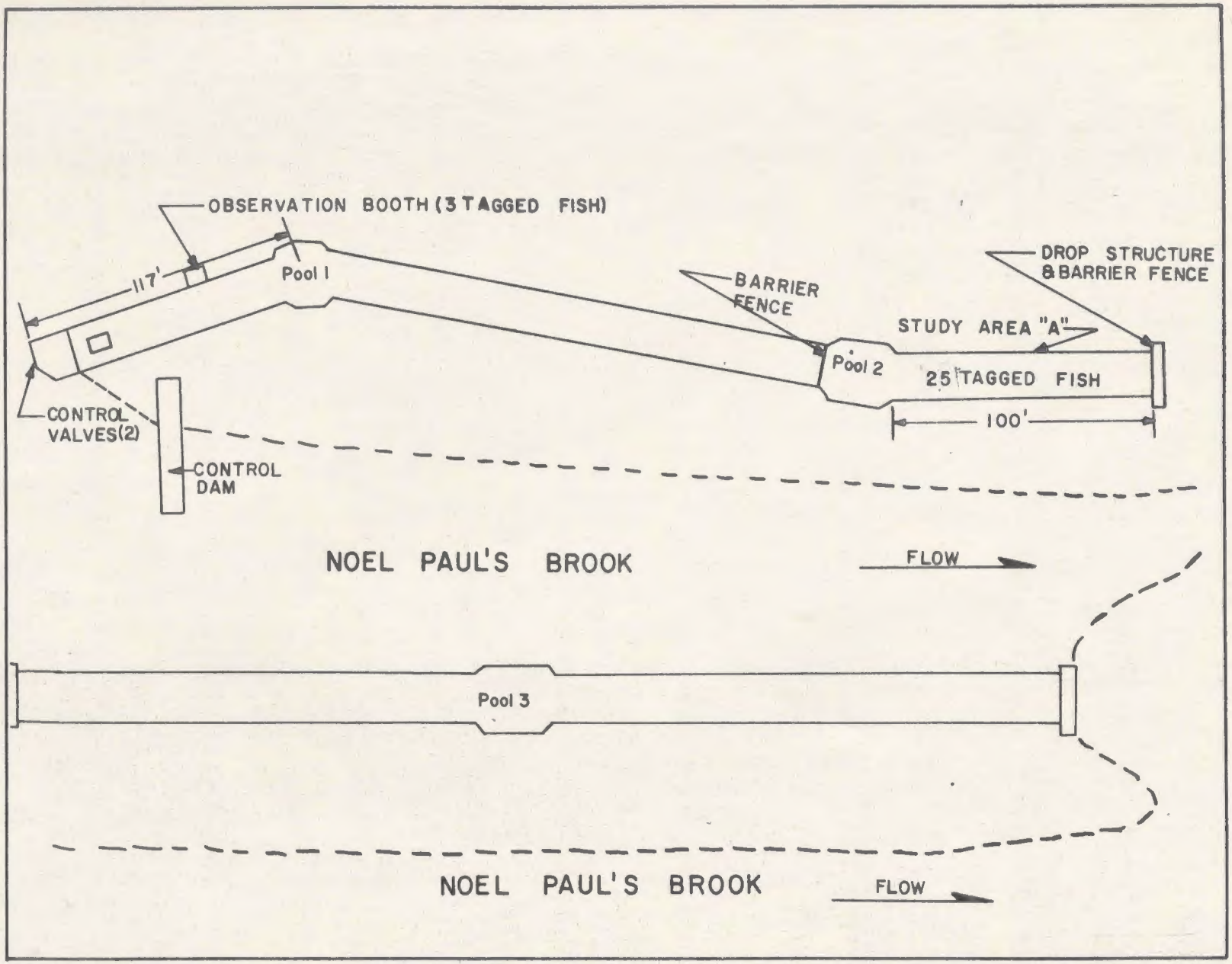


Fig. 6. Diagram showing study area and observation booth along with allocations of tagged fish, Noel Paul's Controlled Flow Channel, 1967.

Table III. Escapements outlined by spawning section, Indian River Spawning Channel and Noel Paul's Spawning Channel, 1965-1967.

Year	Spawning Section	Spawning Area (yd^2) per		Density Index (D.I.)
		Female	Fish	
1965	II	18.6	14.2	0.77
	III	14.1	10.9	1.00
1966	II and III	6.4	5.0	2.19
	IV	18.3	15.8	0.69
1967	A	12.0	6.5	1.17

The machine or "redd plotter" consisted of a piece of 1/4 inch plexiglass placed in a 4 ft. by 6 ft. frame gridded with lathing into 2-foot squares. A long wooden rod graduated at 0.5 ft. intervals was placed in a holder across the rear of the machine. To obtain channel length coordinates, the machine floating over a given section of bed, was lined at right angles to the channel flow but in line with a 2 foot channel marker by sighting along the graduated rod. At the same time, a channel width coordinate was realized by measuring with the rod out from the right hand bank (looking downstream) of the channel. Redd increments were then defined by viewing them through the transparent plexiglass and drawing them on engineering paper at a scale which allowed the paper grid lines and the machines lath grid work to coincide. To ensure consistent and accurate data, one individual plotted all the redds during the three year study except for one or two days each year when a second individual did the

Fig. 7. Atlantic salmon grilse following tagging.

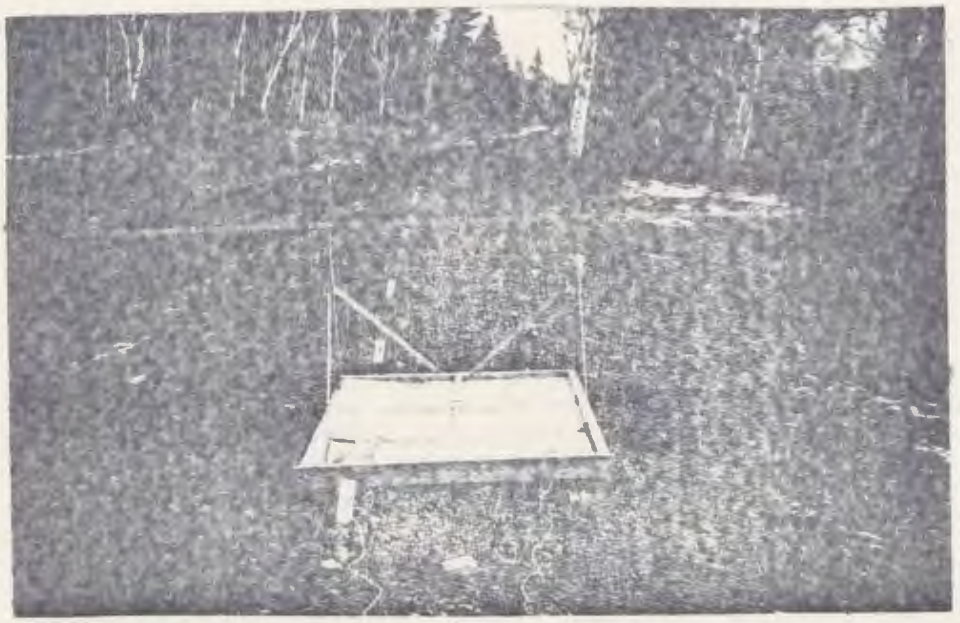


Fig. 8. Redd plotter with graduated rod.

plotting, and also checked redds that were previously recorded. The location of a redd was taken as the centre of the first daily increment built farthest downstream in the redd, the point from which all other nest increments radiated upstream. One plan view map of the channel was composed of a network of 8-foot square quadrats. The point locations for redds were plotted onto this map of grids which covered the six spawning areas. For the purpose of this study, the redd was defined as a spatial entity composed of a series of these daily increments continuous upstream with time.

The hypothesis that redds were distributed at random over the spawning beds was tested at the .05 level of significance in each section by determining if the observed frequency of quadrats containing 0, 1, 2, 3, 4, or 5 redds agreed with the Poisson probability distribution. If every quadrat in each series observed was exposed equally to the chance of containing a redd, then the distribution was considered to follow the Poisson distribution, each quadrat having the population mean as its expected frequency. Since the essential feature of this random distribution is that the variance is equal to the mean, in each section, the discrepancy between the variance and mean was assessed employing the t-test. Where this hypothesis was not upheld because the variance was significantly larger than the mean, then a second hypothesis that redds were distributed contagiously was tested at the .05 level of significance by fitting the negative binomial contagious distribution to the data. The calculated number of quadrats expected for a given integral redd density was compared to the observed values, with the discrepancy assessed using Chi square.

The redd distributions were also examined to determine if fish showed any spatial preference for peripheral or central portions of the channel with spawning at different densities and in different years. For this examination, the channel was divided into three segments of equal width which ran the length of the sections examined. The observed frequencies were compared to those expected based on the null hypothesis that an equal number of redds was placed in each segment. The degree of discrepancy existing between observed and expected frequencies was examined with Chi square at the .05 level of significance.

The evenness of redd building between spawning areas was also investigated in any sections where fish could move freely over two or more of these areas. Based on the null hypothesis that the same amount of redd building occurred on all spawning areas within a section, discrepancies between expected and observed values were assessed with Chi square at the .05 level of significance.

In June, 1967, salmon fry were counted as they emerged from separate regions where adults the year previous had spawned at high density, (Sections II and III), or at low density, (Section IV). Fry progeny were collected with traps placed at the downstream end of Section III and Section IV. The numbers of fry passing by the traps were estimated volumetrically.

B. Physical Aspects of Spawning Distribution

1. Water Temperature, Light and Precipitation

During each of the four daily counts of spawners at Indian River, temperature, percentage cloud cover and kind of precipitation (i.e. rain or snow) were recorded.

A Taylor seven day continuous recording thermograph measured water temperature at Indian River during the spawning seasons. Each of the four daily counts of fish on the grounds was related to water temperature for the particular observation. Before examining the day to day variations in counts and water temperature, it was necessary to account for the seasonal trend with time so that the residual variance could be analyzed independent of time (Andrewartha, 1963; Davidson and Andrewartha, 1948). This was made possible by fitting polynomial curves of the form:

$$Y = a + bx + cx^2 + dx^3$$

for each of the four counts, where Y represents the number of spawners or the water temperature and X the number of days. Temperature and activity deviations from these trend lines were paired and correlation coefficients computed for daytime and nighttime groupings.

Records maintained during 1965 and 1966 for the four daily periods describing cloud cover, rain and snow were inspected. Each factor was classified as coincident with increase, decrease or no change in spawning activity.

2. Water Depth and Velocity

During both years, channel water depth and velocity recordings were taken for each redd with a Watts current metre at the upstream lip of the redd "pot" or excavation at a level considered to represent fish depth before disturbance of the bed occurred. The metre was set to record water velocity 0.4 ft. off the channel bottom. Velocity and depth recordings 0.4 ft. from the channel bottom were also taken uniformly at two foot intervals of channel width and 10-foot intervals of channel length over two of the six spawning areas.

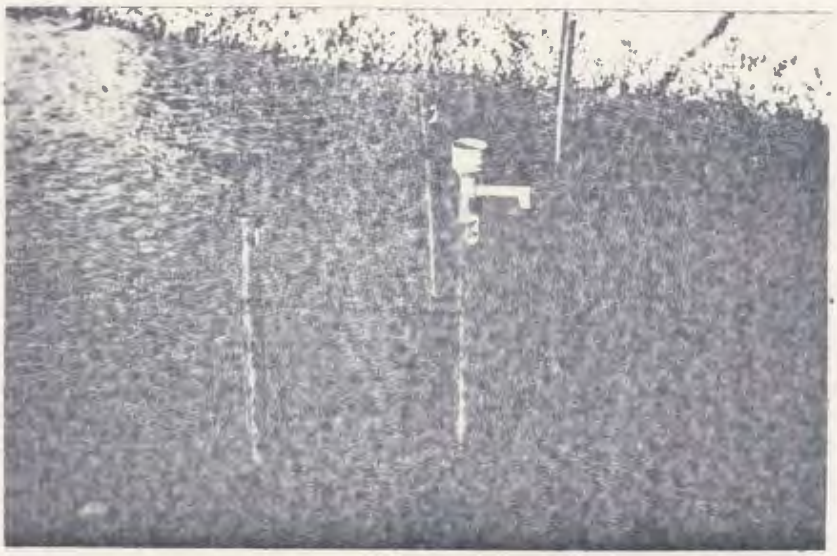


Fig. 9. Close-up of standpipe arrangement during oxygen sampling about test plants (three pipes upstream to left are located upstream of three test plants; Pipe No. 3 represents the downstream control with pump for water removal shown), Indian River Channel, 1966.

Fig. 10. Wire grid of eight foot squares for study of agonistic behavior, Indian River Channel, 1966.

3. Test Egg Plants

In 1965, the relation buried egg plants bore to the channel spawning distribution, was noted. In 1966, dissolved oxygen of intra-gravel water was measured daily at specified points and depths adjacent to egg plants. Sampling was conducted with standpipes and procedures similar to those described by McNeil (1962).

All standpipes used in the study were identical to those devised by McNeil except a 2 inch rather than 3/4 inch inside diameter pipe was used. Pipes were driven into the spawning bed to a sampling depth of 5 to 6 inches. All pipes were pumped out 24 hours before sampling was carried out. To facilitate analysis, oxygen was determined automatically by lowering the probe of a portable oxygen meter directly into the stand-pipe instead of removing a water sample and analysing this by a chemical method. However, before commencing this procedure, the reliability of reading oxygen levels directly within the standpipes with the metre was assessed. Simultaneous oxygen determinations were made in eleven cases and compared. This involved taking an oxygen reading with the metre by placing the probe down into a standpipe followed by the immediate collection of a 300 ml. water sample from the same standpipe for oxygen determination by the Modified Winkler Method. The Paired Comparisons Test was then applied to see if any significant difference between the paired readings existed at the .05 level of probability. At each sampling, water temperature was also taken with the automatic oxygen metre at 5 to 6 inches depth in the spawning gravel.

Thirty egg baskets made of fly screening material and measuring 6 by 6 by 6 inches were filled with fertilized eggs and spawning gravel.

Each year, they were buried so that overlying gravel was 2 or 3 inches deep. The baskets were placed in ten rows across the channel, three plants to a row, and rows one hundred feet apart. In 1966, standpipes were driven into the channel bed three days before any plants were installed at points which were forecasted would be just upstream of the plants but still on the forward slope of the gravel mounds created with burial. One daily reading was taken for three days. Then, the standpipes were removed, the egg plants buried and the pipes reinstalled for an additional five days of reading. At commencement of the eight day series, another standpipe was driven in the spawning bed about 3 feet downstream from each row of egg plants and was not disturbed. Daily readings taken from this control pipe were compared to simultaneous readings taken upstream from each of the three egg plants.

Coloured dyes in solution were used to trace water current patterns about egg plants. Methylene Blue and Rhodomine-B dyes were fed through a piece of glass tubing with a constricted tip which created a well defined dye track underwater.

4. Rock Weirs

The rock weirs constructed in 1965 consisted of a wing or bar on each bank running diagonally offshore and downstream to a point one to four feet from the channel's centreline. The weirs were basically of two types: bars of rock set directly opposite each other (V-shaped weirs, Fig. 12) or bars of rock on banks offset from each other by 5 to 10 feet (staggered weirs, Fig. 5).

The exact replica of one V-type weir built in 1965 was rebuilt in 1966 at the same channel location. Water velocities and water depths

Fig. 11. Redd in testpen; crosses mark upstream and downstream perimeters; pot is visible to left of left cross, Indian River Channel, 1965.

Fig. 12. Crossection of channel showing rebuilt V-type rock weir and locations of standpipes for oxygen reading, Indian River Channel, 1966.

were determined adjacent the weir before and after weir reconstruction; oxygen readings were taken as well but only after reconstruction. Water velocity and water depth were measured at three crosssections: No. 711 was situated 9 feet upstream from the widest portion of the weir; No. 721 was located just inside the upstream mouth of the weir while No. 725 was just below the downstream orifice of the weir. Water velocity was taken at 0.4 ft. from the channel bottom. Dissolved oxygen was read with the metre at three standpipes placed evenly in two rows across the channel: one row was at the weir orifice, while the other was 25 feet upstream of the orifice. At the orifice, two pipes were placed just inshore from each side of the weir to the midstream with one pipe right at the centre of the orifice (Fig. 12). In the upper crossection, two pipes were placed out from shore and one pipe at midstream. All oxygen determinations were taken at 5 to 6 inches below the surface of the gravel.

5. Pool and Spawning Bed Shelters

The distribution of spawners about plywood floating shelters placed within one holding pool and placed on one spawning area was observed four times daily throughout 1966. The pool shelter occupied Pool No. One. Since the number of fish in this section was known (i.e. 21), by counting spawners on the spawning area and fish in the holding pool outside the shelters edge, the number sheltered within the pool could be deduced. The spawning shelter site was selected by use of random numbers and occupied Spawning Area Four. During each observation, the number of fish spawning or residing under this shelter was noted.

Fig. 13. Plywood floating shelter on Pool One, Indian River Channel, 1966.

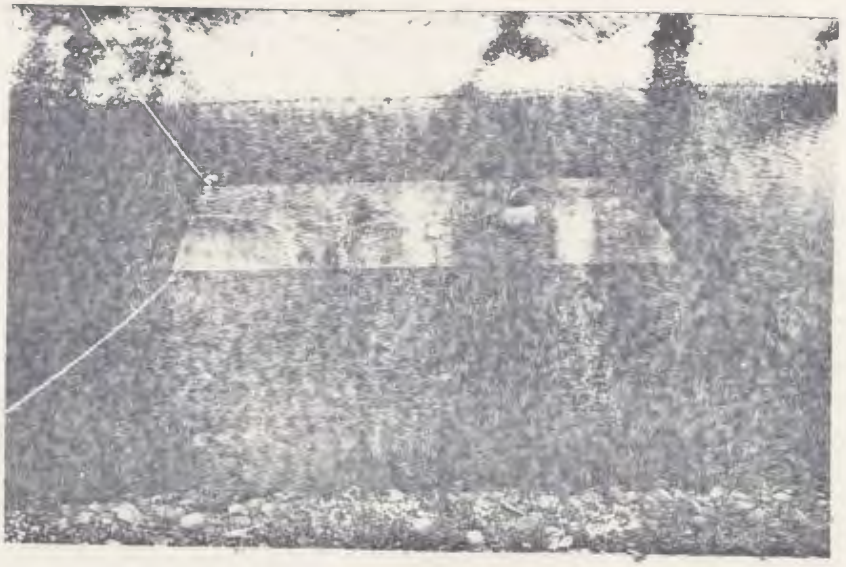


Fig. 14. Plywood floating shelter on Spawning Area Four, Indian River Channel, 1966.

III. RESULTS AND DISCUSSION

A. Biological Aspects of Spawning Distribution

1. Spawning Behavior

General observations made at Indian River and Noel Paul's Brook have established that the Atlantic salmon species spawns quite naturally in controlled flow channels, free of disease or any other adverse factor. Egg checks on females after the spawning season (i.e. mid-November) also showed that egg retention was negligible. If the occasional female was found to still retain eggs, in most cases, stripping or dissection yielded less than five per cent of the estimated ripe egg capacity of the fish. The physical condition of both sexes even at this stage in the spawning cycle was excellent. The gills were always found to be clean, and generally, only males showed any frequency of body fungus. Body abrasions inflicted by commercial nets or by other means were usually minor. During the period of study, adult mortality from predation was unimportant and mainly attributed to the Horned Owl (Bubo virginianus). However, in 1967, a serious outbreak of adult predation did occur at Indian River due to the presence of a small mink population (Mustela vison) which is now being controlled by trapping.

First attempts to study spawning behavior at Indian River Channel were made in September and early October of 1963. Females at this time were still ripening and were engaged at the edges of holding pools in trial diggings which were called trial or test redds because they received no eggs. Fish remained in holding pools during the day but were active on the spawning beds at night. The use of lamps to observe their behavior was fruitless because the light beam alarmed them. However, once the

population approached spawning maturity in mid October, it was less disturbed by light and positioning of fish on the beds by this method became possible.

Spawning activity on the beds responsible for the formation of true redds (or redds containing eggs), mainly occurred at night (Figs. 30, 31, 32). Nonetheless, in all years excepting 1965, it was possible to observe some daylight activity during three or four days at peak spawning, weather and water conditions permitting.

Daytime observation centered on only a few females which were actively digging a pit or egg receptacle at one location. They were usually accompanied by one male and frequently there were one or more fish located a short distance, usually downstream, from the resident pair or tenants to the pit. This observation established the general sequence of the spawning act starting with the digging action by the female on the bed, including one orgasm between the pair and ending with the covering of the fertilized eggs in gravel by the female. Many of the spawning details established by Jones and others at close range with tank observation in Britain could not be fully examined during the observations at Indian River which were conducted mainly at distances of 10 to 20 feet from the subjects by standing on one of the edges of the channel. However, a "trial run" during 1967 of the newly built observation chamber at Noel Paul's Brook did supply some further pertinent information although most of the operation was aimed at exploring and remedying operation problems before conducting a detailed spawning study in 1968. The general spawning behavior observed with the females and male placed in this facility was similar to that observed in Indian River Channel.

Just before spawning, the female was observed to remain at one locality on the bed and converge digging or cutting actions to one particular site thus eventually creating a depression in the gravel. The details on digging are similar to those described by Jones (1959) and shown photographically for Noel Paul's observation chamber in Fig. 15. At this stage, the male regularly took position beside the female but one or two feet from her with his nose usually a few inches to a foot below her nose. Cutting by the female continued with varied frequency and duration, the courting male usually becoming very attentive during this procedure. Eventually, the female settled down onto the area she had been working, the male moved down into the depression with her; both opened their mouths and orgasm commenced. During orgasm, both partners arched their backs and raised their tails (Fig. 16). While in this posture, the female was quite motionless but the male was often noted to shake or shudder quite violently and repeatedly. At this point, a stream of eggs and a cloud of milt could sometimes be seen being shed simultaneously into the bed depression by the female and male respectively. Following orgasm, the male left for an indefinite period. Meanwhile, the female moved upstream one or two feet and began cutting the bed once more, burying the eggs just deposited downstream and also starting to build a new egg receptacle further upstream for another possible spawning. In one case in the channel, the same female was observed to repeat the entire spawning act at the new location. This meant that egg nests or pits were laid down in a series upstream with space and with time.

Generally, a female which settled onto one site of the bed and dug periodically at the bed furnished sufficient stimuli to interest

Fig. 15. Strips of 16 mm. movie film showing one complete digging sequence by female, [illegible] aul's Observation Chamber, 1967 (strip courtesy MUN University Extension Department).

a male into taking up the typical male position. If he occupied this position consistently without leaving the female for periods greater than one minute, it was assumed that a sexual bond had been established and that these fish were tenants actively courting and mating.

Females were witnessed to dig at varied frequency in the Noel Paul's Observation Chamber before and after spawning. In Fig. 17, the average number of digging sequences made by females for varying intervals of time before and after orgasm, are shown by plotting the mean frequency at the midpoint of the timed interval. Usually, in the 50 minutes before orgasm, digging frequency tended to increase somewhat towards orgasm and then gradually decrease with time after orgasm. One detail which was masked by averaging in the figure, was the digging frequency to cover the egg nests in the few minutes following orgasm. The frequency during that interval was actually higher than at any other period.

The interval for the orgasm was timed in only one case at Indian River Channel but six orgasms involving two females were timed in Noel Paul's Chamber. At the channel, the total time for both members of the pair to complete spawning was 19 seconds but this in the writer's opinion was relatively longer than most of the untimed orgasms. Orgasms in the chamber ranged 9 to 22 seconds while the average was 16.3 seconds.

Many incomplete spawning acts were witnessed both in the channel and observation chamber. Occasionally, the female would begin digging in an area, but no male would be attracted to the female and the sequence would never proceed beyond that point. In a few cases, sequences were much more complete due to the presence of a tenant male. They included cutting, courting and mating as described above but without the

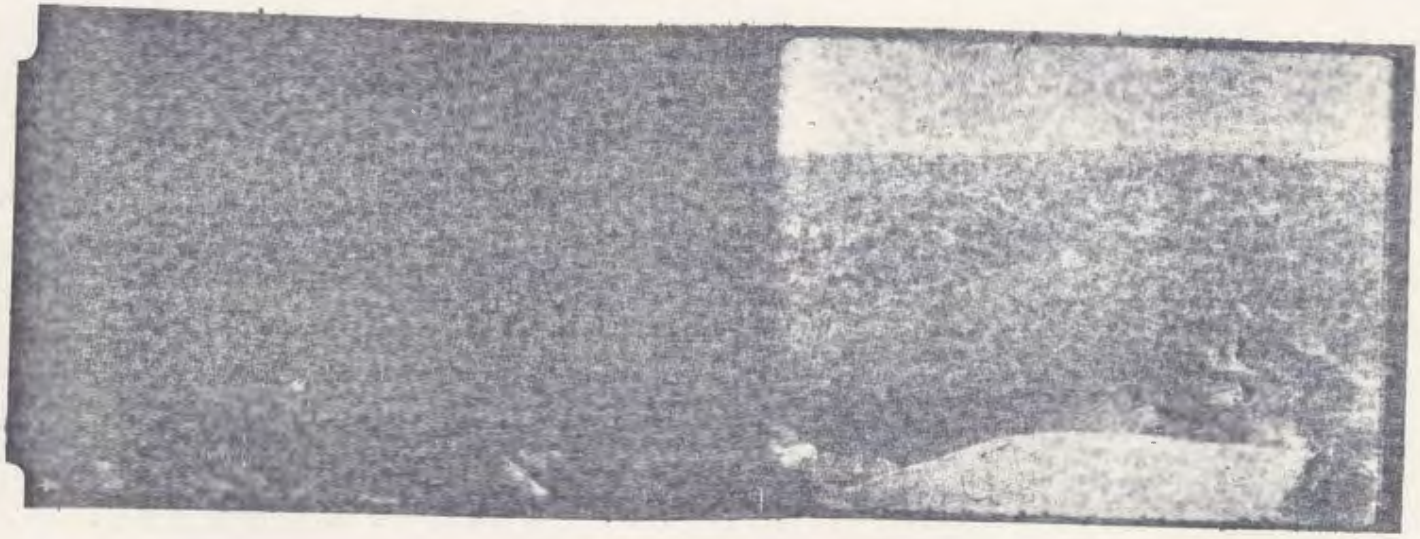


Fig. 16. Spawning pairs participating in two separate orgasms. Female cannot be seen behind male in spawning to left but arrow indicates an egg while white cloud of milt exuded by male is visible in left hand corner. Both members of pair visible in mating to right, Noel Paul's Observation Chamber, 1967 (reproduced from 16 mm. film taken by MUN University Extension Department).

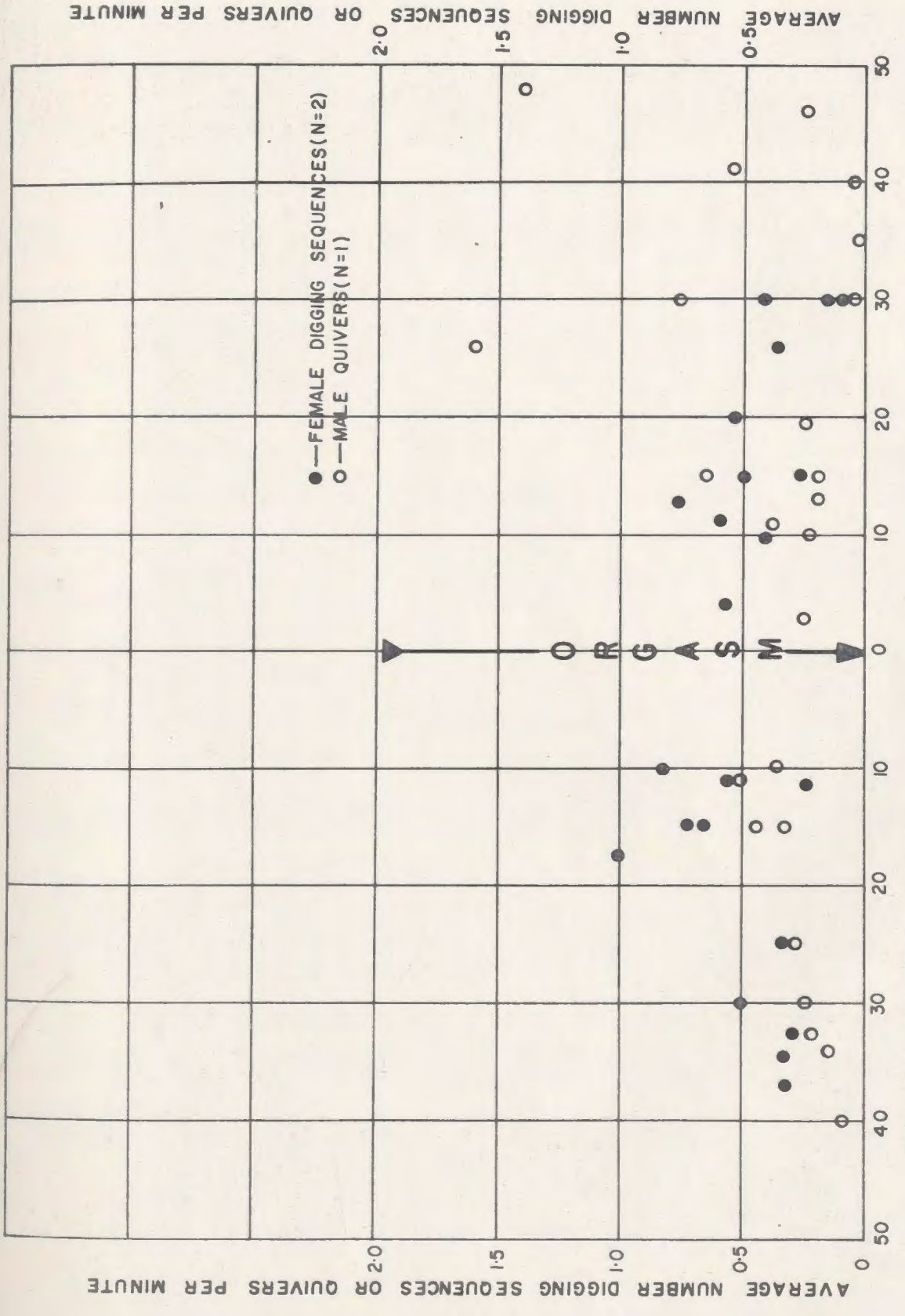


Fig. 17. Frequency of female digging sequences and male quivers before and after orgasm, Seal Paul's Observation Chamber, 1967.

simultaneous shedding of eggs and milt or the subsequent upstream digging and covering. This phenomenon appeared very much like the "false orgasm" which Jones and Hall (1954) witnessed during their tank observation.

The male shudderings described earlier were noted in other circumstances besides orgasm. In most of these other cases, the male moved in beside the female and shuddered in a manner apparently identical to that observed at orgasm, but without the ejection of sperm. Jones and Hall have proposed that when a male quivers against an active female, she will give a typical female response of "cutting". However, on no occasion was a male observed to release this or any other response in a female at the channel or in the chamber.

An interesting phenomenon was noted in the frequency of these shudders produced by the male in the chamber (Fig. 17). The shudders increased in frequency up to orgasm but then tended to fall off somewhat for the first 15 minutes after orgasm only to often increase very substantially in the 15 to 75 minute period following orgasm, followed by decrease after this period. This usually occurred hours before the next orgasm. It is wondered if this notable increase could be an "after discharge" as mentioned by Tinbergen (1953), which is caused in situations where a drive (such as the reproductive one) is strongly activated.

Paired spawners often showed hostilities to other fish which came within the vicinity of their redd and their sexual territory. During defense, relative positioning of mates seemed quite important. In territories defended on the right and left portions of the channel bed, the female occupied a location next to shore with the male on the downstream outer side. The male in this position defended mostly the radius

to the midstream side, neglecting the most adjacent bank. Intruders very rarely moved up on shallows between the female and the channel bank where they supposedly were more vulnerable to tenant male or female attacks. Territories defended in midstream usually found the male further downstream from the female than in marginal spawning but usually occupying one side of her - that side where most of the foreign adult activity seemed to be centered and/or that side offering the largest expanse of female and redd vulnerability. Occasionally, when the female occupied a central position with no foreign distractions to either side, the male mainly occupied a position just below and roughly in line with the long axis of the female's body.

During the study, males were noted as the most aggressive in their reactions to intruders. Generally, they would not allow interested intruders to approach the female or the redd area beyond a general perimeter. Females for the most part were more docile while attended by a male but became quite aggressive towards any intruder whenever the resident male left the redd. Hostilities did not always take the form of active attack and bodily contact between tenants and intruders. Aggression in male residents was mainly threatening gestures as when a tenant male drove away intruders by drifting back downstream, tail first, past the tenant female towards the trespasser. This in itself, was often sufficient to cause the intruder to withdraw but if not, the further movement of placing his body at a diagonal to the current across the foreigner's nose frequently resulted in the intruder's departure. On other occasions,

the male would dart upstream or downstream after a particular intruder sometimes snapping his jaws and even engaging in bodily contact with the outsider. Sometimes, such active attacks precipitated into "dog fights" and reciprocal snapping and biting would occur.

Aggressive actions by the resident females like the diagonal movements of the male tenants were often used to shoulder intruders away from the vicinity of the redd. Active attacks sometimes occurred but biting or bodily contact between females and outsiders was seldom noted. The most pugnacious attacks by any resident female were usually directed towards another female who began cutting in bed just upstream or beside the residing female's pit. Most types of aggression by the female usually brought about withdrawal of any invader to her territory.

On numerous occasions, spawning pairs were noted to show threat behavior with other intruders to their territory. Groups of salmon parr could often be seen occupying a position usually a few feet downstream from the pair. Some adult males showed no notable reaction to their presence while other adult males chased them away. Female tenants showed similar responses towards the parr. However, parr chased and displaced by either member of the pair usually returned to their former position.

Whenever the channel holding pools were seined during the season to check adults for ripening, considerable numbers of parr and trout were recovered. Many of the male parr, upon running the thumb backwards over the belly exuded white milt of similar colour and consistency to that of ripe adult male fish. Moreover, dissection of some of the stomachs of the

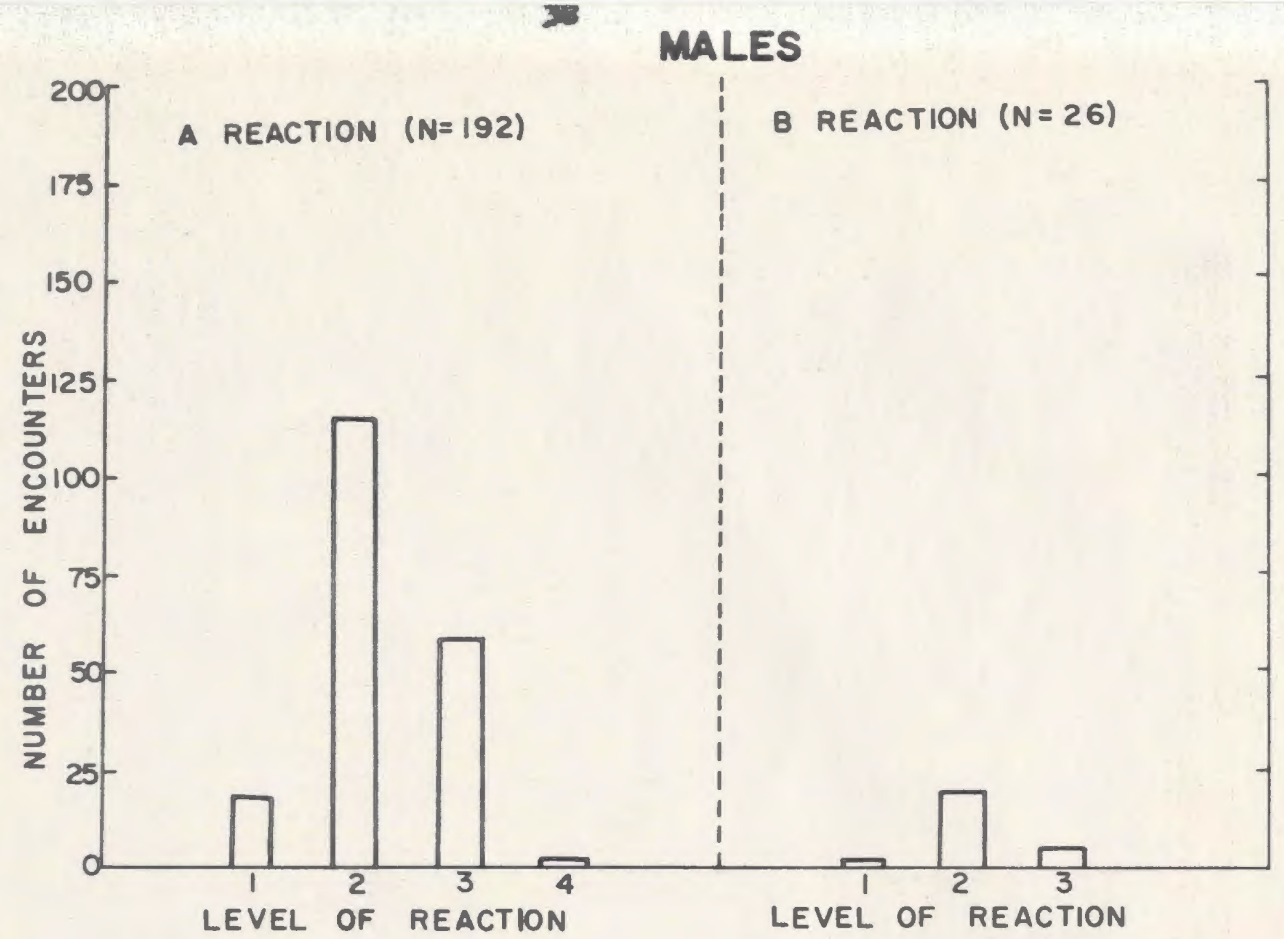
parr and the trout, showed they were usually filled with salmon eggs, the number consumed dependent on the size of fish. For this reason, an effort was always made to remove the largest parr and trout from the channels before the spawning season.

Jones (1959) states that ripe male parr when accompanying the pair are active participants in the spawning act and contribute sperm to eggs. Although he discovered that male parr were ineffective in egg fertilization except when accompanied by the adult male, he believes they may ensure a larger probability of fertilization than what might prevail if pairs spawned in their absence. In two orgasms between pairs, two or three parr stationed downstream were noted to move in under the female but in either case, it was not discerned whether their activity led to orgasm with the adults, egg predation, or both. This was because the parr usually disappeared from sight down between stones in the bed, just beneath the pelvic region of the female.

Studies on sockeye salmon (Oncorhynchus nerka) indicate that as high as 1:15 ratio of males and females result in almost as high fertilization as if parity of the sexes is maintained (Matheson, 1962). Hence, considering that the sex ratio in the populations of Atlantic salmon is running as low as 1:3 ratio of males to females, it is doubtful if this contribution by salmon parr is that important to ensuring fertilization. In fact, in view of the egg predation noted, it would seem advisable to follow this more closely since this may be a factor just as important to egg mortality where high spawning densities are prevalent as the factor of redd superimposition.

In the objective analysis of territorial behavior in 1966, the format of necessity had to be very general because it was found impossible to get close enough to every pair under these semi-wild conditions to consistently observe the finer threat movements (such as any fin or opercle movements). This analysis would also have been more informative if intruders could have been identified but all observation was conducted with untagged fish in Section III. Although observations were attempted in that same year on the 21 tagged specimens occupying Section II, this lower complement of spawners in such a short section provided insufficient day spawning activity for the study envisaged. It was also assumed in the analysis that the territorial responses of residents were little affected by any changes in factors such as sex ratio, fish size, bottom type, water depth, and water velocity because channel and experimental design kept them quite constant with space and time.

Fig. 18 shows the type, intensity and frequency of all observed aggressive and retreat reactions released in male and female tenants by the presence of intruders in their breeding territories. A-type or aggressive reactions predominate for both members of the spawning pair indicating a dominance and hence a stability of the pair on a territory despite intrusions. But, if one compares the reactions of the two sexes, the female is portrayed as the most static and yet the most docile of the pair. Less than five per cent of the total female reactions recorded were retreat reactions while males were less stable with more than ten per cent of their reactions recorded as b-type. At the same time, ninety per cent of the female reactions to intruders were second level intensity or lower while ninety per cent of the resident male



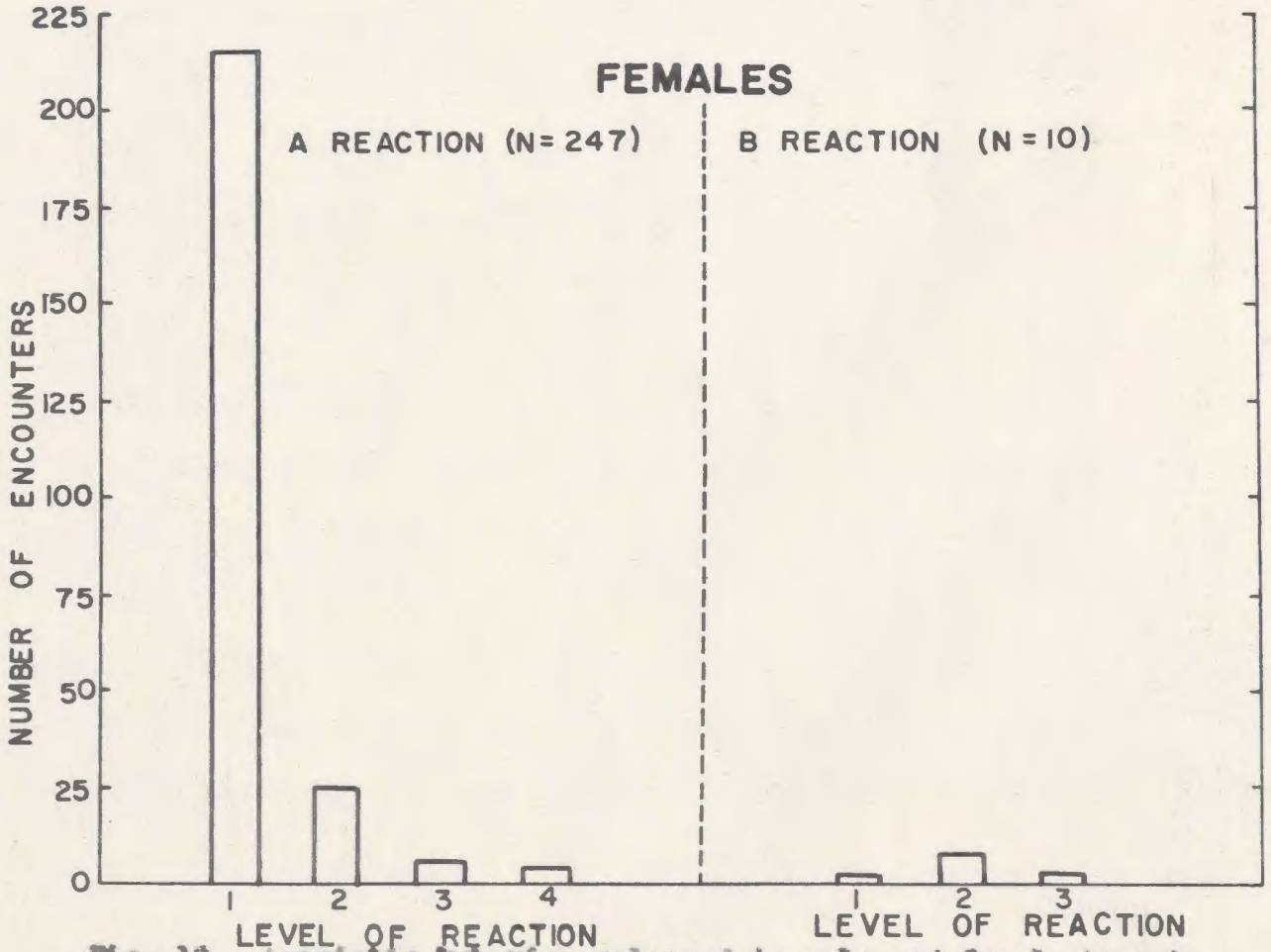


Fig. 16. Agonistic behavior released in male and female tenants of territory, Indian River Channel, 1966.

encounters were second level or higher. The large number of 1(a) - reactions for tenant females resulted because as previously mentioned the female when accompanied by the male was usually quite docile in her reactions to an intruder while the male generally registered higher level (a) - reactions to the same intruder. On the other hand, whenever the male left the female alone on the territory she became more active in defence registering higher level attacks towards any further intruders during the male's absence. This accounts for the higher total number of reactions recorded for females in Fig. 18.

During the four daily counts conducted at Indian River in 1965, and 1966, and at Noel Paul's in 1967, the time available for observation of each fish was very limited. There was no opportunity to watch individual spawnings during the lantern checks at night when most of the spawning was known to occur. However, if a sexual bond was indicated between a pair by their relative positioning and stability over one part of the bed, and if this bed site was subsequently found from the redd plottings to contain egg pits concomitant with the pair association, it was assumed that the tenants had engaged in at least one spawning act at that site leaving eggs deposited in at least one pit at that site.

Since redd activity in the channel was only plotted once daily, the term "increment" was used to describe the area of bed placed into pits or egg nests during a 24 hour period. In establishing the relationship, unless the female of the pair was sited right at the point where a current redd increment was plotted, then the observation was disregarded.

While locale tenancy predominates in Fig. 18, the incidence of (b) - reactions means some reservation must be exercised in assuming that

an association of male and female under these circumstances indicates one or more egg pits deposited within an increment by the pair. The probability that a fish sited exactly on a current increment spawned there is according to the recorded frequencies higher for females than for males due to his higher rate of replacement.

The data collected at Indian River in 1965 and 1966 on increment - tenant associations was not as complete as that collected on Study Area A at Noel Paul's in 1967 (Fig. 19). At Indian River, a female-male association had to be presumed usually on the basis of their presence during only one daily observation, although sometimes, two and three of the daily checks were found to have the female in attendance but often in the company of another male. The more extensive Noel Paul's records showed that females were sited on 36 of a total of 45 increments placed into 15 redds. In only 3 of the 36 were there different females sighted on the same 24 hour increment. In the rest of the plottings, the same female was sighted daily on increments an average of 1.8 times or during approximately one half of the 4 daily checks. The males were noted as more heterogeneous in their relationships with particular increments and females. Although they were sighted over 33 of the 45 increments, 18 involved more than 1 male and averaged 2 different males during the four daily observations. Seventeen of the 18 increments were also recorded to be occupied by 1 tenant female and associations with different males was the rule. Also, in 4 cases simultaneous associations with more than one male were observed. On one increment, actual association was not observed between the tenant female and the males. The remaining 14 increments involved 1 male, spotted only once during the 4 daily checks, 13 of which were occupied by a tenant

female but in 2 of these cases, the male was not observed on the increment at the same time with the female. The other remaining increment was the only example where one male on two checks was the exclusive attendant of a tenant female. Thus, sighting of a female on a concomitant increment appears to be a reliable indication that an increment containing one or more pits belongs to one and the same female. However, with males, there is much more likelihood that the increments are contributed to by more than one male with some of the supposed point associations never materialising in his mating because of this sexes higher rate of replacement on territory. Data describing males should be interpreted with this reservation in mind.

Fig. 19 illustrates the above relationships diagrammatically. From the illustration, the following generalisations were formulated:

1. Some females spawned at only one redd location.
2. Some females spawned at more than one redd location.
3. Females and males showed low specific preference for mates during spawning.

It has long been recognized that the females of many species of salmonids spawn in more than one location of a spawning bed. Although Matheson (1962) has shown a very strong connection between female sockeye salmon (Oncorhynchus nerka) and one specific redd site in studies he carried out at Hansen Creek in Alaska, Hobbs (1940, 1948) has observed separate redds placed by trout species in several separate areas on natural spawning grounds in New Zealand streams. Riengold (1965) also recorded a case where a female steelhead trout (Salmo gairdneri) built two redds at different locations.

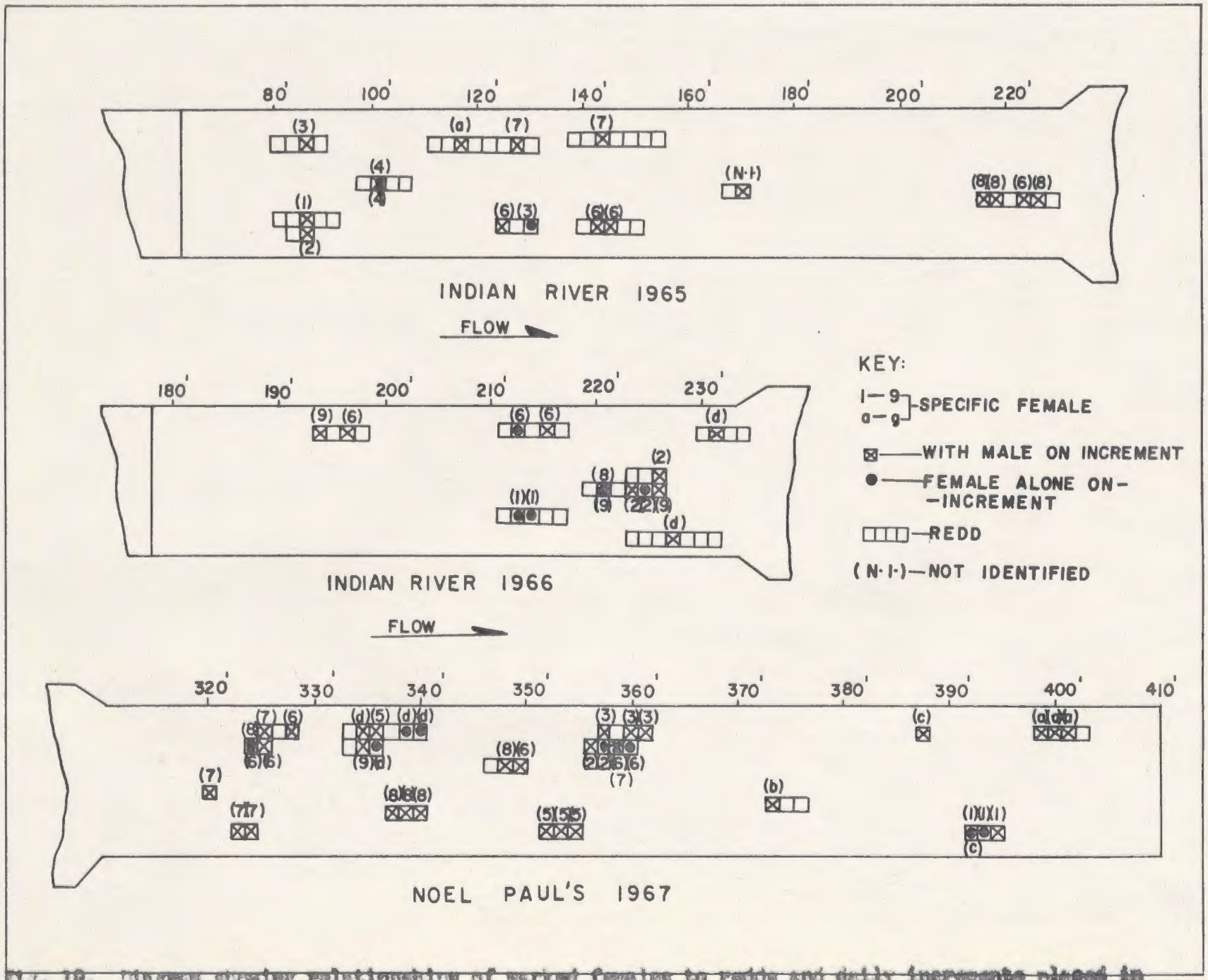
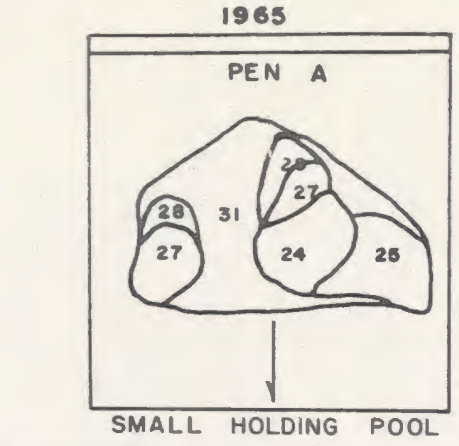
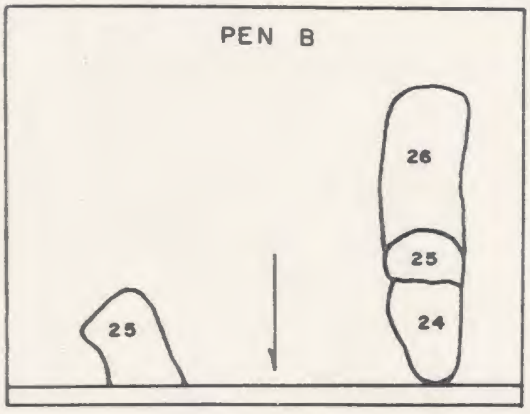


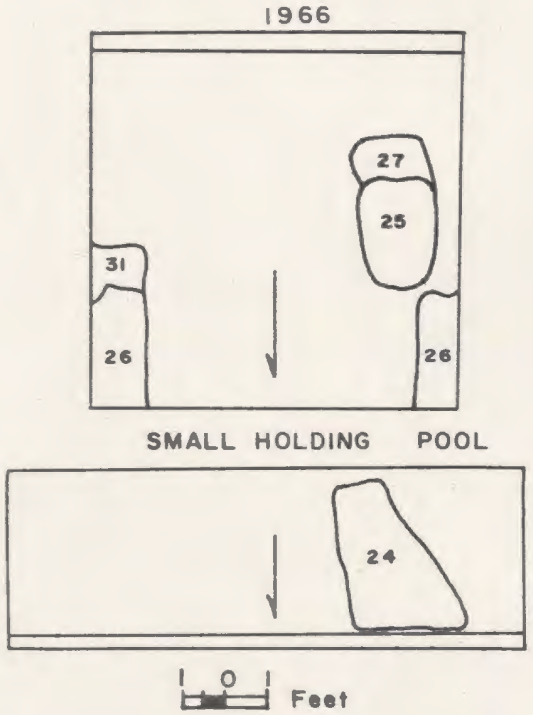
Fig. 19. Diagram showing relationships of marked females to redds and daily increments placed in spawning bed, Indian River and Noel Paul's Spawning Channels, 1965 - 1967.

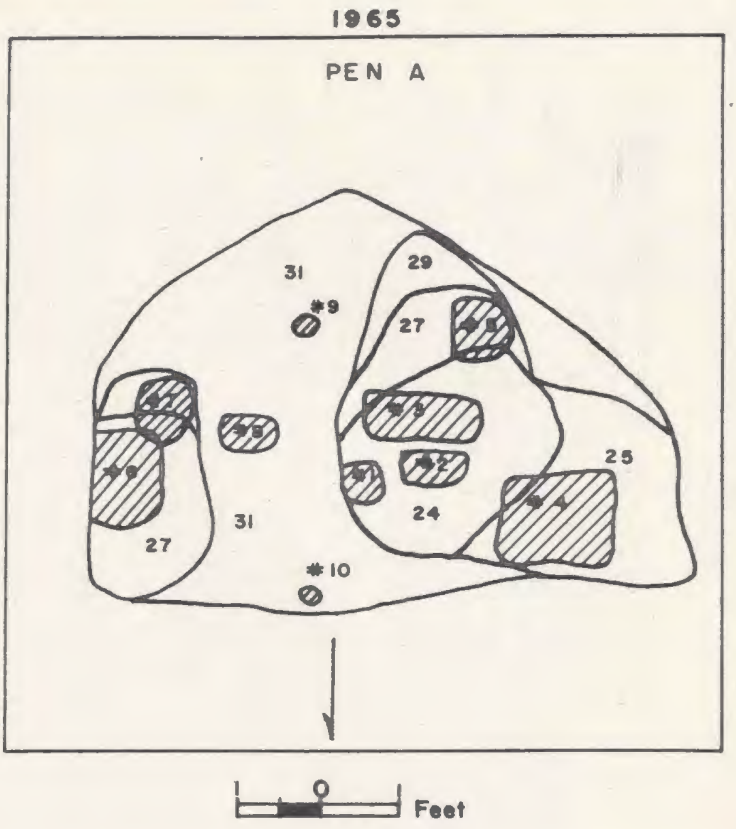
In the studies with test pens at Indian River Channel in 1965, both isolated Atlantic salmon females chose two separate sites for spawning. Two redds are indicated in Pen B. However, in Pen A, redd increments initially placed in two separate locations were finally incorporated into one redd. In 1966, increments were placed by one female at four different locations with one increment being built at the downstream edge of a shallow part of the holding pool off the surface of the platform.

On the spawning beds containing several females (Fig. 19), observations were far from complete at Indian River and Noel's Paul Brook because fish tended to be quite elusive to observation especially at Indian River. Of the observations made, certain females placed all noted pits within the same redd (e.g. at Indian River, female 8 in 1965; at Noel Paul's, female a, 3). In other cases, females placed pits within several separate redds (e.g. at Indian River, female 6 and 7 in 1965, and 6 in 1966; at Noel Paul's, female 5, 6, 7, 8). More important, there is reason to suppose that some of the redds observed casually as a continuum upstream with space and time may not be composed of a series of pits and increments all built by the same female. Often, increments composing a redd were attributed to different fish (e.g. at Indian River in 1966 at co-ordinate 226 centre or "C" female 9, 2; at Noel Paul's, co-ordinate 329 left or "L" looking downstream, females 6 and 7, co-ordinate 339L, females 5 and d). Furthermore, some of these females did not place their daily pits and increments in one uninterrupted succession. At Indian River in 1966, female 9 at 226C in her spawnings was attributed with only the first and part of the second to last increment placed in this redd









PEN A

DATE 1965 OCT	PIT NO.	NO. EGGS	PIT AREA (Sq. in)	PIT VOL. (Cu. in)	AVERAGE DEPTH OF PENETRATION IN INCHES	DAILY REDD AREA INCREMENT (SQ. YD.)
24	1	37	25	75	5.5	0.69
	2	98	40	120	7.5	
	3	503	144	720	6.5	
25	4	444	196	980	7.5	0.56
27	5	351	49	225	4.5	0.32
	6	515	144	864	5.0	
28	7	340	80	200	4.0	0.09
31	8	147	32	170	5.5	1.44
	9	11	4	12	5.5	
	10	17	N.T.	N.T.	N.T.	
24-31	STRAYS	29	N.T.	N.T.	N.T.	
AVG.	10	246	79	374	5.6	0.62

Fig. 20. Test pen studies with isolated pairs giving details on redd building. In diagrams to left dates of increments composing redds are given. To right, further details on number, size, location and depth of egg pits in increments of redd in Pen A, 1965, are given in diagram and table, Indian River Channel, 1965, 1966.

with one and possibly two increments from female 2 intervening; female 2 was also observed to spawn elsewhere. Earlier in 1965, female 8 was associated with an increment in the lower part of a redd in the vicinity of the 220 foot mark and then twice more in the upstream region of the redd. However, intervening the series was one increment containing one or more pits attributed to a different female (female 6).

The non-exclusive relationship between females and the entire sequence of increments composing any spatial redd entity was also reflected when examining the duration of spawning in females in light of the periods over which increments were placed in redds. The three females in the test pens (Fig. 20) completed spawning within a period of three to eight days, the two year average being 6.3 days. In examining the redd plotting data, it was apparent especially in 1965 that a few of the redds (mostly those started at the beginning of either season) were often completed over a period of 2 to 2½ weeks. In these cases, the additions to the redd were built progressively upstream, in a series of successive daily increments, each series interrupted by delays in building of one or more days. In a few cases, there were redds composed of more than two of these series. Hence, it becomes obvious, that if one considers the spawning interval in the female as even averaging one week, then these series of daily increments separated by sizeable time gaps in building cannot all belong to one female but must be built by several different females. At Noel Paul's Brook, a similar situation was noted but the period during which the two females built their redds in the observation chamber tended to be lower (average 1 - 2 days) although the period over which the channel redds were built tended also to be considerably less.

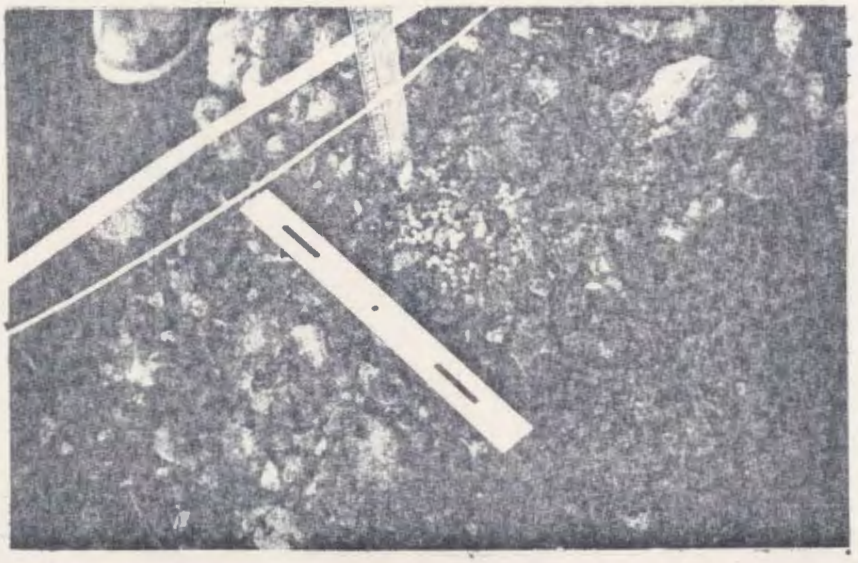


Fig. 21. Egg pitt excavated in redd within Test Pen, Section I, Indian River Channel, 1966.

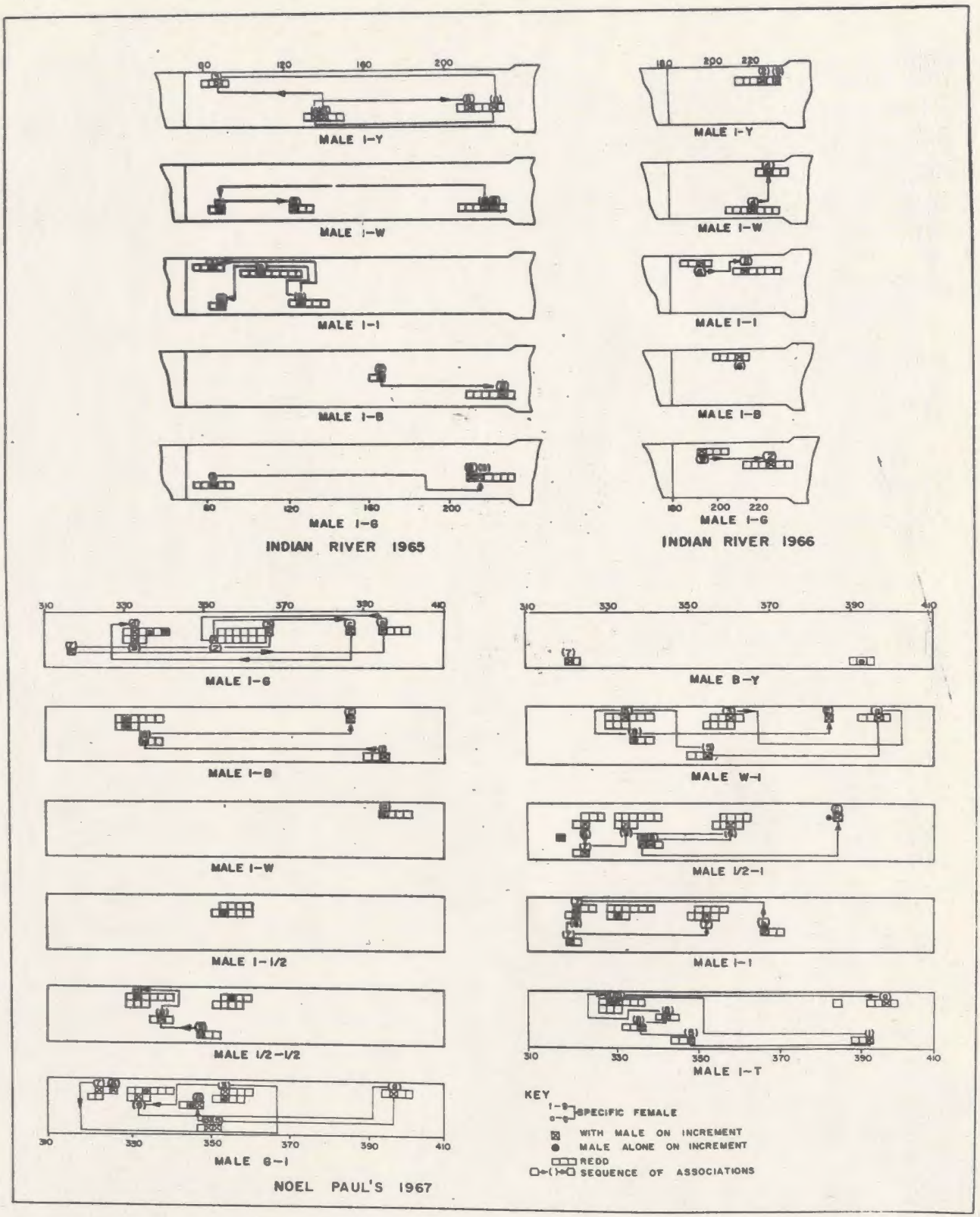


Fig. 22. Diagram showing sequence of redd building by tagged males which spawned at more than one redd location, Indian River and Noel Paul's Channels, 1965 - 1967.

This phenomenon may in part be the result of late ripening females replacing early maturing but spent females on the redds since it is known that the spawning population or escapement in the channel does not always ripen simultaneously. In 1965, holding pools were seined four days after discovery of the first egg deposition in the channel. At that time, all the males were mature, but only one-fifth of the females were "running ripe". Nonetheless, there were 18 redds already underway in the channel each with an average of 2 increments completed.

Fig. 19 was inspected to determine if redds containing successive increments in space but separated in time by several days did belong to different females. For such an examination, Indian River results are not that complete. Twenty to thirty time gaps between spatially successive increments did occur in the section of tagged specimens in 1965 and 1966, but unfortunately, the females which contributed to the increments on both sides of the gaps were never both observed. However, in Noel Paul's data collected from Study Area A, the associations observed were complete about two time gaps that occurred between increments in redds. A redd at 350 left centre (LC) looking downstream contained successive increments separated by a time gap of one day which belonged to two different females ♂ and ♀. At 338 L, successive increments in the upstream part of the redd separated by a gap of 6 days belonged to two separate females ♀ and ♂. Thus, it is apparent that time gaps between continuing series of increments may represent a change in tenant females building onto the redd. However, the converse statement that a change in females working on redds indicates a time gap is not true. Again, at Noel Paul's, female ♀ replaced female ♂ on a redd at 33RLC and female 2 replaced female ♂ at 36OLC without any time gaps being evident.

The annual sex ratios which existed in the two channels indicate that the association between a particular male and female is not likely a very stable one over the spawning season. Less than one quarter of the fish in Indian River escapements were male (Table II) while less than half those at Noel Paul's were male. This means that in several cases, males must have engaged in matings with more than one female and the relationship must have involved successive polygamy on the part of the males.

This premise is borne out in sex associations observed over the three year study. In Fig. 22, all supposed matings are outlined for males.

It is quite evident that most of the males spawned with more than one female. Occasionally, a male was noted to associate with one of a group of his assumed partners repeatedly on more than one increment belonging to the same redd (at Indian River, 1965, male 1-Y, 1 - G; at Noel Paul's, male 4 - 1, G - 1), or more frequently on increments belonging to different redds (e.g. at Indian River, 1965, male 1-W, in 1966 male 1 - W; at Noel Paul's, male G - 1, W - 1, 4 - 1, 1 - 1, 1 - T). The noted record for polygamy was male 1 - G at Noel Paul's who associated with seven different females out of the total available number of thirteen. However, within this group, there were also males observed as almost sexually inactive (e.g. 1 - W, 1 - 4).

Male 1 - Y at Indian River in 1965 is an example of how inconsistent pair relations can be with time even with a female at a given redd location. This male commenced relations with female 6 but before continuing to spawn with this same tenant the following day,

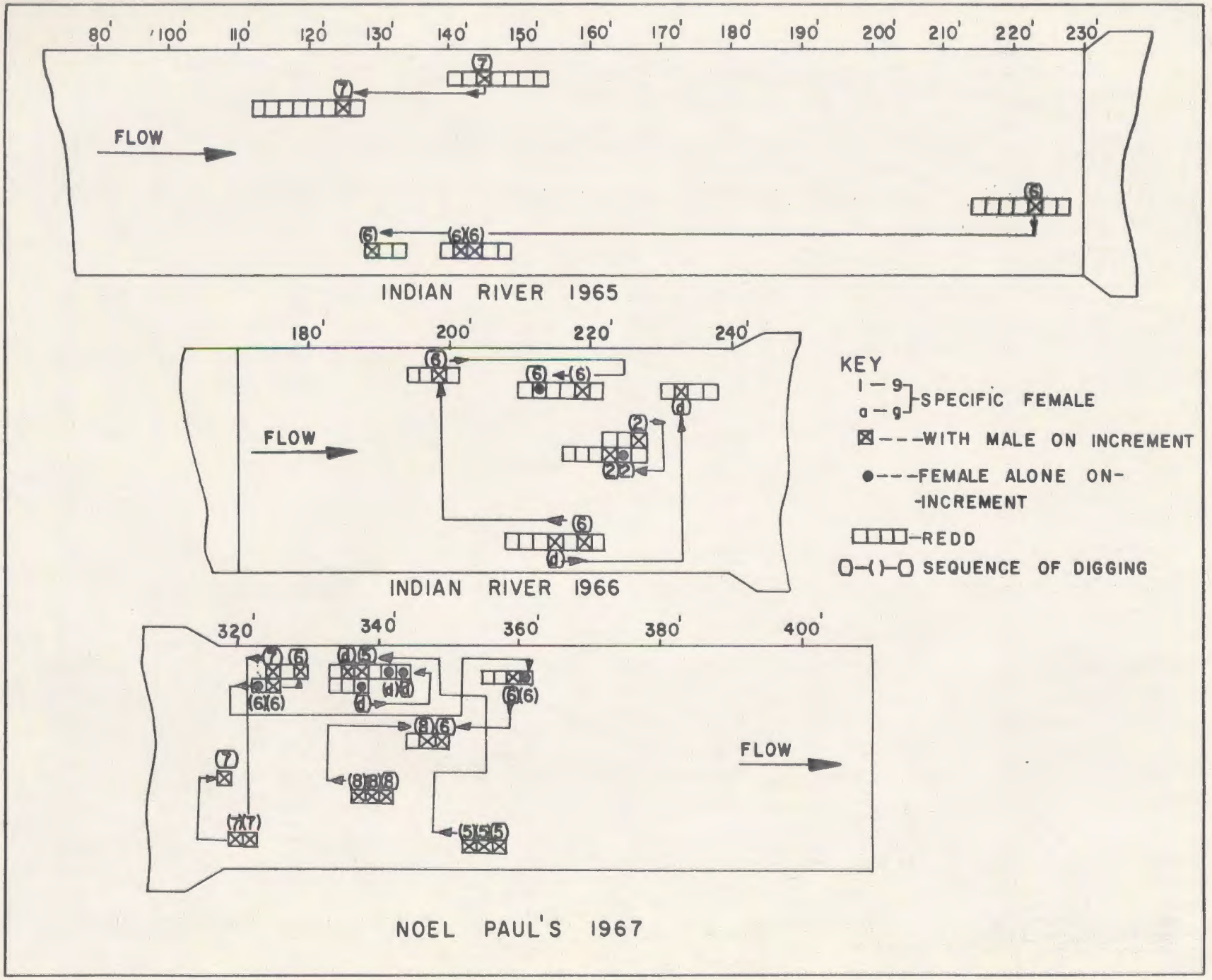


Fig. 23. Diagram showing sequence of redd building by tagged females which spawned at more than one redd location, Indian River and Noel Paul's Channels, 1965 - 1967.

was active with female 3 fifty feet further upstream, then with female 8 ninety feet further downstream. Upon his return and association again with female 6, he then moved downstream to repeat residence on the redd with female 8. One would suspect that as the sexes become more even that sexual bonds between particular pairs would become more permanent involving several spawnings. However, male polygamy is still very much the rule even at Noel Paul's Brook where the sex ratio more closely approximates parity.

In Fig. 23, associations for females spawning at more than one redd location are shown. Frequently, females placed pits into the same redd increments contiguous spatially and temporally but placed increments at other redd locations before and/or after these spawnings (e.g. at Indian River, 1965 female 6; Noel Paul's, female 5, 8, and 7. Occasionally, females were witnessed to only spawn in one increment at each redd location but this is probably more the result of incomplete data (e.g. at Indian River 1965, female 7; 1966 female d) than to actual behavior since the incidence of this is lower at Noel Paul's where records were more complete.

In summary, it appears that Atlantic salmon exhibit a definite territorial behaviour during spawning but it is quite transitory both in regard to spawning locale and mates. This to a large extent must prevail because of a sex ratio favouring females which for complete egg deposition and fertilization requires that most males mate with several different females. Although the associations between increments and females were not completely recorded, it would appear very doubtful that females always place all their nests at one redd location or that a spatial entity of successive pits and increments composing the so called "redd" can be considered to belong wholly to one particular female spawner.

2. Spawning Density

Although the 1965 part of the experiment was designed to have approximately the same light spawning density in Sections II and III, adults entering the lower channel from the river after the segregations had been made tended to make the density in Section III somewhat higher than Section II (Table III). On the other hand, the density imposed on the main 1966 escapement in Sections II and III was over twice that of either 1965 sections and over three times that of Section IV during 1966.

Table IV and Figs. 24 and 25 shows the results of the analysis of the patterns of redd distribution in the various spawning sections during the two seasons. The frequencies of quadrats with different integral densities ranging from zero to five redds are listed for each section in the table.

In 1965, the redds built by tagged spawners in Section II were distributed according to a Poisson series and thus in a random manner (Table IV), but not by the rest of the untagged spawners in Section III. The variance in Section III was significantly larger than the mean. Additional sub-sampling was carried out in Section III to determine whether the over-dispersion was occurring consistently everywhere or specifically in one or more spawning areas. In order to preserve a large working sample, this region was sampled five times, each time excluding only one of the spawning areas from the calculation. The results obtained from the different samples were marginal or poor examples of the Poisson ($0.1 > p > 0.001$), except in the case where Area No. Four was deleted. This sample agrees with the hypothesis that the

Table IV. Atlantic salmon redds in 8 foot square quadrats for various spawning sections and the theoretical Poisson distribution, Indian River Channel, 1965, 1966.

No. redds per quadrat	1965			1966			
	Section II D.I. = 0.77	Section III D.I. = 1.00	Section III excluding Area Four	Section II D.I. = 2.19	Section III D.I. = 2.19	Section IV D.I. = 0.69	Section IV excluding Area Four
0	23	109	83	3	14	89	63
1	17	49	41	5	13	41	28
2	2	18	13	4	11	11	9
3	0	9	7	1	3	3	2
4	0	1	0	0	1	0	0
5	0	0		1	0	0	0
Total	42	186	144	14	42	144	102
t-test	0.2>p>0.1	0.05>p>0.02	0.2>p>0.1	0.7>p>0.6	1.0>p>0.9	0.1>p>0.05	0.5>p>0.4
(0.05 level)	random	non random	random	random	random	random	random

redds are distributed at random since it follows the Poisson series (Table IV, Column 4). Spawning Areas Two, Three, Four, Five, and Six of Section III were also examined separately, bearing in mind that the sample size in some cases was small (as low as 22). Areas Two, Three, Five and Six were portrayed as typical Poisson distributions (P range of 0.25 to 0.70) while Area Four was atypical (.05 p .02) with the variance exceeding the mean.

When the variance is significantly larger than the mean, there are a number of other distributions that may be used to describe biological distributions. Bliss (1953) suggests the Negative Binomial Distribution is a very adaptable one and one which often describes events much better than the Poisson. Unlike the Poisson, this distribution is applicable where the occurrence of an event is associated with increased probability of recurrence of the event. It is defined by two parameters: the population mean (μ) and a positive exponent (k), their magnitude dependent on the amount of contagion. The negative binomial converges to the Poisson as the contagion diminishes. Hence, the importance of aggregation in redds depends on the relative values of K and μ (Bliss, 1953; McNeil, 1967). The population variance (σ^2) and mean are related empirically in the negative binomial distribution by:

$$\sigma^2 = \mu + \frac{\mu^2}{k} \quad \ldots\ldots\ldots (1)$$

(McNeil, 1967). Thus, as μ becomes small or K becomes large $\frac{\mu^2}{k} \rightarrow 0$, the variance and mean tend to approach equality, and the relationship converges to that of the Poisson.

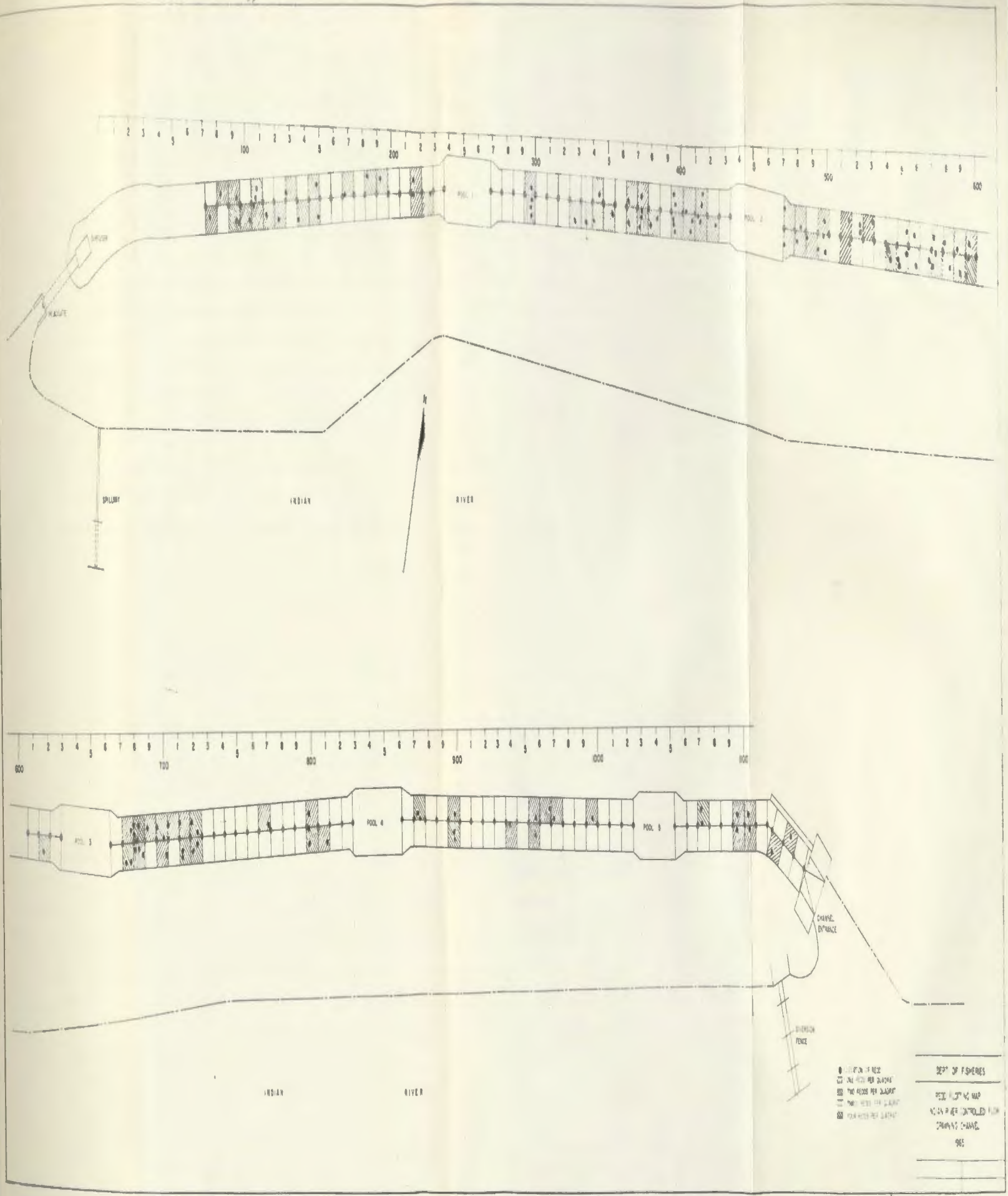


Fig. 24. Diagram showing locations of redds within quadrats and integral redd densities of quadrats, Indian River Channel, 1965.

Results of fitting the Negative Binomial Distribution to the two cases of overdispersion along with this typical Poisson Distribution of Section III excluding Area Four are shown in Table V. Referring to both Tables IV and V, the redd distribution of Section III excluding Area No. Four appears to follow the negative binomial distribution or Poisson distribution equally well (both .2>p>.1) while Section III including Area Four follows the negative binomial much better (.25>p>.20) than the Poisson (.05>p>.02). Data of Area Four was found to closely approximate the negative binomial distribution (.50>p>.30) but not the Poisson distribution at all (P~.02). The influence of Area Four on the values of K is notable. The relative value of K is at its highest in Section III

Table V. Distribution of Atlantic salmon redds in 8 foot square quadrats for various spawning sections compared to the negative binomial distribution, Indian River Channel, 1965.

Location	$\hat{k}$	$\bar{x}$	pI^2
Section III excluding Area Four	3.60	0.61	.20 p .10
Section III including Area Four	2.37	0.62	.25 p .20
Area Four	0.77	0.67	0.50 p .30

excluding Area Four, lower when Area Four is included and least where Area Four is treated separately indicating that Area Four is the main region where significant contagion probably exists. Data of Section III excluding Area Four did fit the Negative Binomial Distribution as well as the Poisson but the relatively large value of $\hat{k}$ compared to $\bar{x}$ in Table V

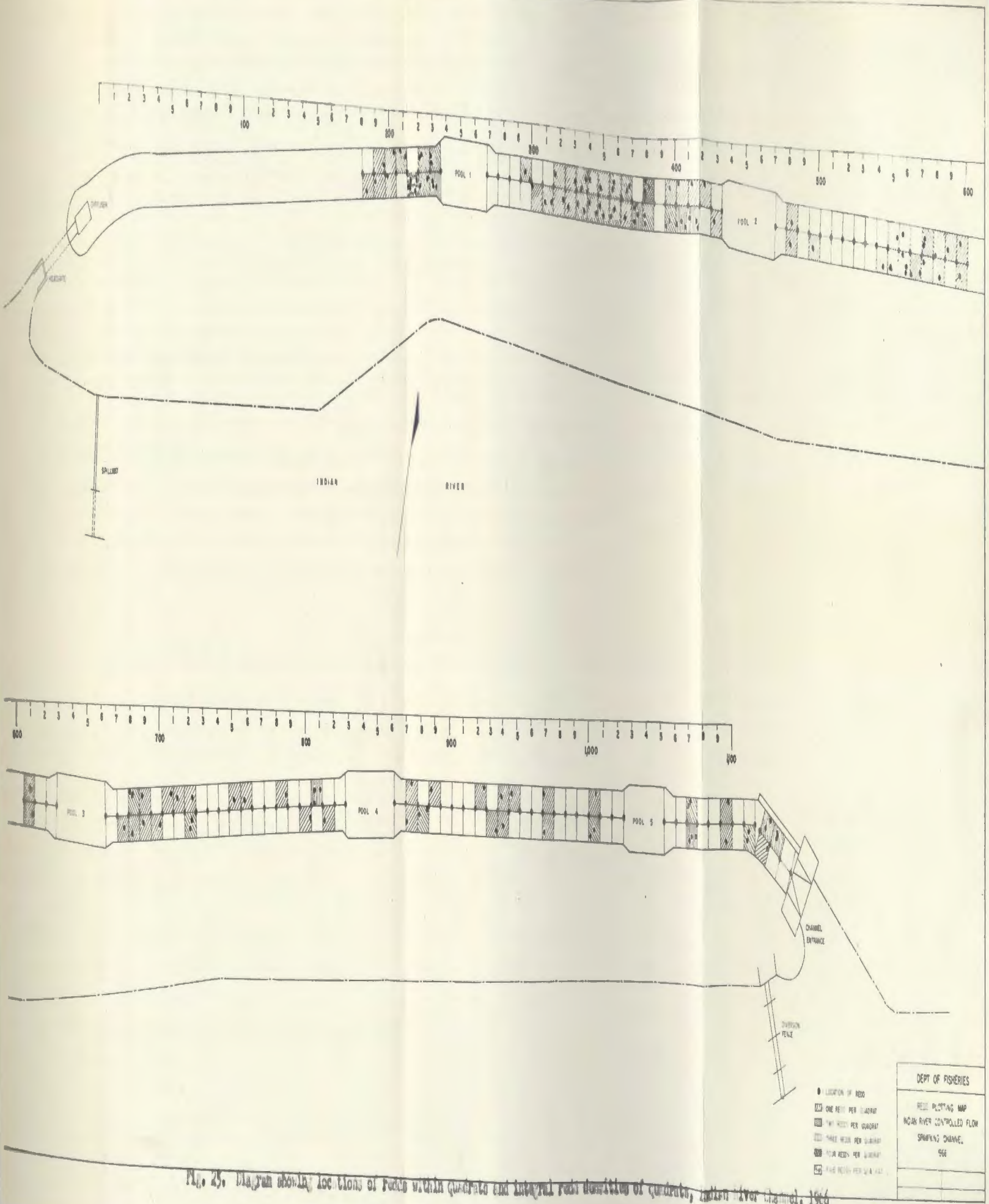


Fig. 25. Diagram showing locations of redds within quadrats and interval redd densities of quadrats, Indian River channel, 1966

suggests that contagion here is slight (McNeil, 1967). Hence, from the Poisson and Negative Binomial analysis of the 1965 data, it is deduced that at the relatively low spawning density of one fish per 11 to 14 square yards, the distribution of spawning in the channel may be considered acceptably random in all areas excepting Area Four where significant aggregation of redds was detected. Upon inspection of this area, redd clumping was evident in the upper portion of the area just upstream from one of the rock weirs constructed within the channel. The possible association of this weir and redd clumping is examined later in a separate study on weirs.

In 1966, (Table IV, co. 5 and 6) redds were built in both sections with differing densities in a random manner, the agreement of each redd distribution with the Poisson series being generally better than the year before. Despite doubling the density over the previous year, and despite the presence of the rock weir on Area Four, significant redd aggregations are not evident. In fact, the P values of t indicate that the observed redd distributions approximated the theoretical Poisson series more so when spawning density was high than when spawning density was low (Area Four excluded).

The degree of discrepancy existing between observed and expected frequencies for each section of width examined in the channel with Chi square is shown in Table VI. The number of redds observed in each section did not differ significantly from the expected frequencies at the 0.05 level for any of the 1965 sections examined based on the hypothesis that an equal number of redds would be placed in each segment of width.

Table VI. Observed redd frequencies at given width intervals from right bank (looking downstream) compared to frequencies expected, Indian River Channel, 1965, 1966.

Width Interval	1965			1966		
	Section II D.I. = 0.77	Section III D.I. = 1.00	Section III excluding Area Four	Section II & III D.I. = 2.19	Section IV D.I. = 0.69	Section IV excluding Area Four
Right periphery	8(8)	42	33	34	31	22
Mid stream	6	45	35	13	13	9
Left periphery	7	29	20	20	28	21
	21	116	88	69	72	52
Chi square	.7>p>.5	.2>p>.1	.2>p>.1	.01>p>.005	.05>p>.025	.05>p>.025
0.05 level	non-sign	non-sign	non-sign	sign	sign	sign

However, the 1966 redd distributions were such that the hypothesis of even distribution with width at the 0.05 level of significance was rejected. Right and left portions were more heavily utilized than the central section with a lower probability of distribution being due to chance in the high density area ($P < .01$). This more uneven distribution in Sections II and III cannot be attributed to the high spawning density in 1966 data or in earlier data collected on this aspect. In Table VII, P values obtained with Chi-square are presented for the years 1963 to 1966. In 1963, a light spawning density (D.I. = 0.99) prevailed in the channel but redds were concentrated on the left periphery but not significantly so ($.10 > p > .05$). However, in 1964, with the entire channel spawning density almost as high as in Sections I and II in 1966, the distribution was very even with only slight aggregation on the right periphery ($.70 > p > .50$). It is, therefore, reasoned that the uneven distribution of redds with channel width is in no way associated with spawning density.

Bank vegetation cover may provide an explanation for this spawning distribution with width. Chambers, et al (1955), from research conducted on Pacific spawning grounds found that Chinook Coho and Sockeye species tended to select areas where cover was available when other factors were suitable but would spawn in absence of cover. During construction of Indian River Channel, bank vegetation and topsoil were removed especially from the right bank. With the addition of foot and vehicular traffic, vegetation has been very slow returning to this side. This may partially explain the somewhat lighter concentration of spawning on the right side in 1963 when vegetation was sparser here and the more even utilization of

Table VII. P values derived from applying Chi square to width interval data, differing in spawning density, Indian River Channel, 1963 to 1966.

Year	Density Index	$P(X)^2$
1963	0.99	.10 p .05
1964	1.95	.70 p .50
1965	0.77	.70 p .50
	1.00	.20 p .10
1966	2.19	.01 p .005*
	0.69	.05 p .025*

* Significant at .05 level

all portions in 1964 and 1965, as the growth became better established on the right bank. The 1966 distribution which is significantly lower for spawning at mid-stream may also be deduced from this line of reasoning, as vegetation continued to increase on both banks. However, it should be noted that the very reverse trend in edge spawning has been noted with Pacific pink salmon at Jones Creek in British Columbia (Mackinnon, 1961). In the initial period after channel construction when tree cover was removed, pinks favoured the channel periphery. With a later return of growth, spawning at mid-stream increased. The possible association of the edge effect at Indian River with preference of water velocity and water depth by fish will be examined in a later section.

Results of the study on consistency of redd density between sections where fish could move on a volitional basis over two or more

Table VIII. Comparison of number of redds observed to number of redds expected on sections involving free dispersal of adults over two or more spawning areas, Indian River Spawning Channel, 1965, 1966.

Spawning Area	1965		1966	
	No. redds observed	No. redds expected	No. redds observed	No. redds expected
Two	31	26		
Three	37*	25	22	20
Four	28	26	20	21
Five	11*	25	16	20
Six	9	14	14	11
Total	116	116	72	72
$P\chi^2$	.01> p>.005		.7>p>.5	

* Largest deviations from expected

spawning areas are presented in Table VIII. For 1965 spawning, large deviations were detected within Section III on Areas Three and Five. Although redds on both areas were randomly distributed according to the Poisson analysis, utilization of Area Three was heavier while Area Five was lighter than expected according to Chi square if one assumes even utilization of all spawning areas. The 1966 data, on the other hand, supports the hypothesis of equal placement of redds between the four spawning areas constituting Section III.

The uneven deposition of redds on Area Three and Area Five during 1965 is probably connected with the concentrations of fish residing in adjacent holding pools from whence they move to spawn. It was noted

that a proportionately large number of fish resided in Pool Three, a sparse population in Pool Four, while Pool Five was between these extremes. The differences are mainly attributed to the shallow nature of Pool Four. Although all the pools contained floating shelters, in this shallower pool, fish not directly beneath the shelter could be seen even when they were right on the bottom. This seems to account for the lighter redd concentration than expected on Area Five which is downstream from Pool Four and for the heavier concentration than expected on Area Three above Pool Three. In 1966, Area Three and Area Five still had heavy and light redd concentrations, respectively, but not at levels which were significantly different from those expected.

The distribution of locations of new redds and the locations of increments onto new redds was also examined with time. Figure 26 illustrates the occurrence of new redds during the spawning season with the period over which redds in any area began divided roughly into three equal time intervals. Each of the first two intervals contain the same number of days as often does the last interval except when there were deficiencies or surpluses of one or two days with division. In such cases, the last interval often contained less or more days than the first two.

During 1965, the occurrence of new redds in the four upper areas tended to start earlier, extend later and be heavier at mid-season compared to redd building in the lower two areas. The frequency of new redds was highest during the last time interval in Area Five but highest in the first interval on Area Six. In 1966, in the comparably low density area, with the exception of Area Three, the peak frequency of new redds occurred during the first third of each area's redd building period and were

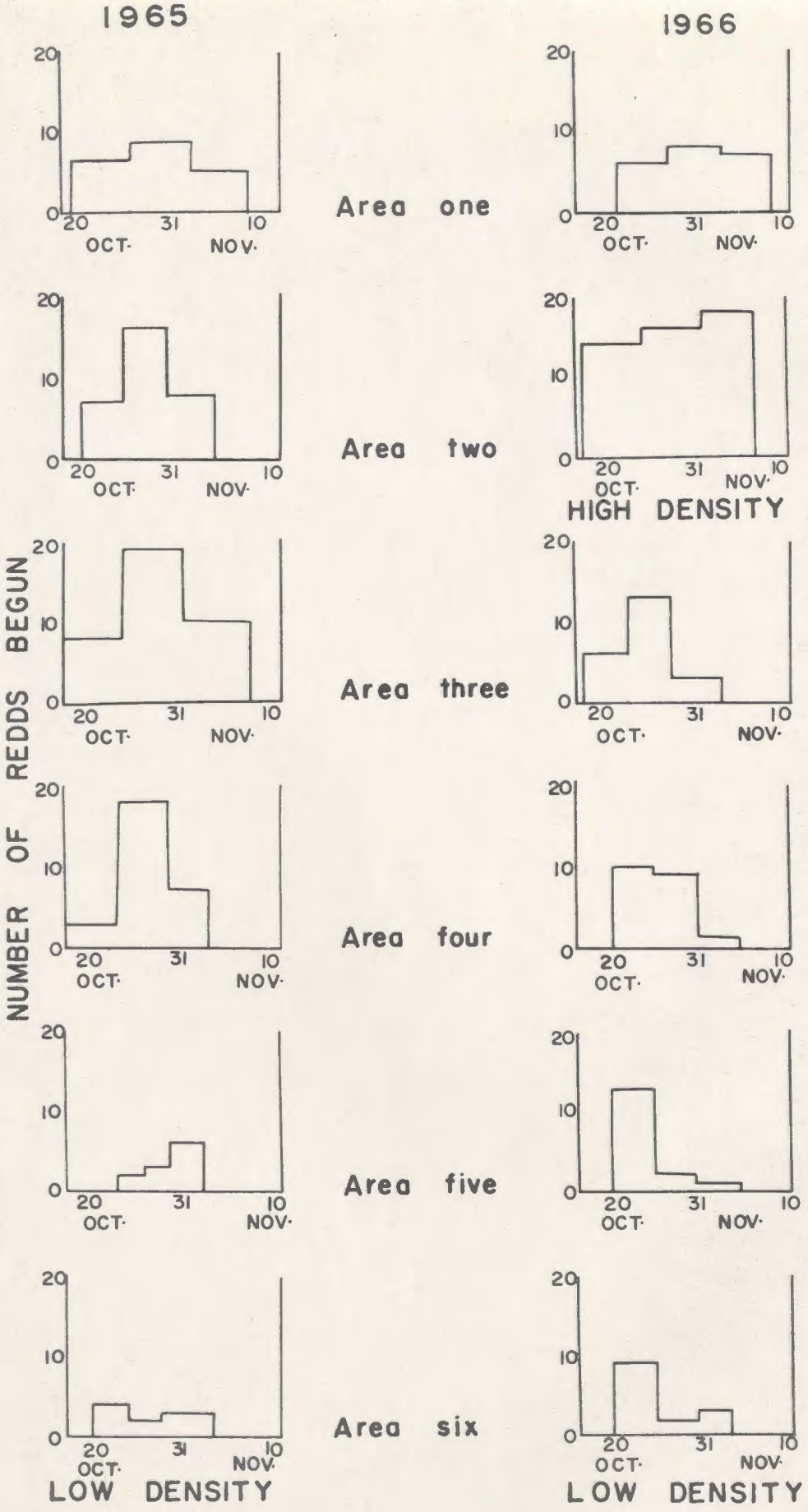


Fig. 26. The distribution of locations of new redds with time by spawning area, Indian River Spawning Channel, 1965, 1966.

proportionately lighter for formation of new redds towards the end of the season than in 1965. On the other hand, in the two areas held at high density, most of the new redds were not begun at the first of the season but mainly occurred during mid-season and the end of the season with the peaks for Area One being mid-season and for Area Two the end; redd building also extended later on these two areas than in any of the other areas. Thus, in 1966, a large proportion of the new redds built in the latter third of the season, occurred in the high density areas. Figs. 31 and 32 also indicate that proportionately more of the redd area was laid down in the latter part of the season in the high density section than in the low density section.

As a further check on the pattern of redd activity with time, the spatial adjacency of increments built on the same day were inspected to determine if digging with time might be highly localized or clumped, a manifestation which would not be detected when examining the distribution of locations of new redds in total as was done in Table IV. For the most part, this inspection indicated no marked aggregation of increment building for any particular day at any particular point, area or part of the channel. During 1965, and most of 1966, daily workings tended to be well distributed throughout the channel with time with no decided concentration of increment building in any given section or area. However, during the latter week of the 1966 season the increments built, although spatially distributed, were mainly placed in the upper high density sections and were negligible in the low density section downstream.

The point locations of the initial increment in each redd were compared for the years 1965 and 1966. Only seven redds or roughly five

per cent of the total number deposited in 1966 were started on the exact site where seven redds occurred the year before. Hence, redds did not notably tend to start in exactly the same spot on the beds from year to year.

It would appear that more random spawning distributions were attained in 1966 with the most random distribution occurring in the high density sections but that the greater crowding here prolongs and alters redd activity somewhat with time (Fig. 26). Furthermore, Fig. 29 indicates that adult activity expressed in numbers of fish was modified since the peak of midnight activity occurred four days later in fish held at high density than at low density. For any of the four daily spawning activity checks, no more than two thirds of the spawners were ever observed on the beds within the low density sections while no more than six tenths were observed on the high density sections. Uneven sex ratios, territorial behavior and gradual ripening within the escapements are factors which probably regulate the intensity and duration of annual spawning at most density levels. However, in 1966, it is believed that the females all ripened more quickly relative to the beginning of true spawning than in 1965. Netting of holding pools in 1966 one week after building of the first true redd indicated that most females were ripe while Fig. 26 demonstrates relatively more of the total new redd building during the same year in the first seven days of spawning on any area than during 1965. Perhaps more fish spawning earlier on the beds means less temporal staggering and overlap in the spawning territories and more randomized spawning distributions. It is understood that in managing Pacific salmon spawning channels, keeping adults out of the channel until a sufficient ripe escapement has accumulated results on their release to the channel

in a lower overlap of territories with time than if they were allowed to straggle in as they arrive at the entrance. Although redd activity in Fig. 26 appears higher at commencement of 1966 than of 1965, examination of Figs. 30, 31, and 32 does not indicate an increased proportion of fish on beds during the same interval in 1966 over 1965. However, intensity of redd activity at the start of the 1966 season may not necessarily be directly related to fish numbers but rather to a higher degree of ripening in that year within fish frequenting the riffles.

Superimposition of redds must mainly come about when females complete spawning at a particular redd location, and move on, and are replaced in that area by other females with an overlap existing between past and present spawning territories. Succeeding female spawners place eggs in nests in untouched area just upstream to previous increments placed in a redd, in altogether new area away from previous digging, or in redd area already laid down. The last alternative inevitably leads to nest superimposition and damage to previous egg nests while the first two frequently develop into overlap if digging progresses upstream into abandoned redd area.

The effect of spawning density on redd size and redd superimposition in 1965 and 1966 is shown in Table IX and Fig. 27. It can be seen that as density increased, the redd area which each female utilized in depositing her eggs diminished. It is also apparent that the amount of redd area which females superimposed during spawning varies directly with density of spawners in each section. At low densities (D.I.<1.0), redd area per female in a section remains above 2 square yards regardless of year or section considered. However, at higher density (D.I.>2), the same

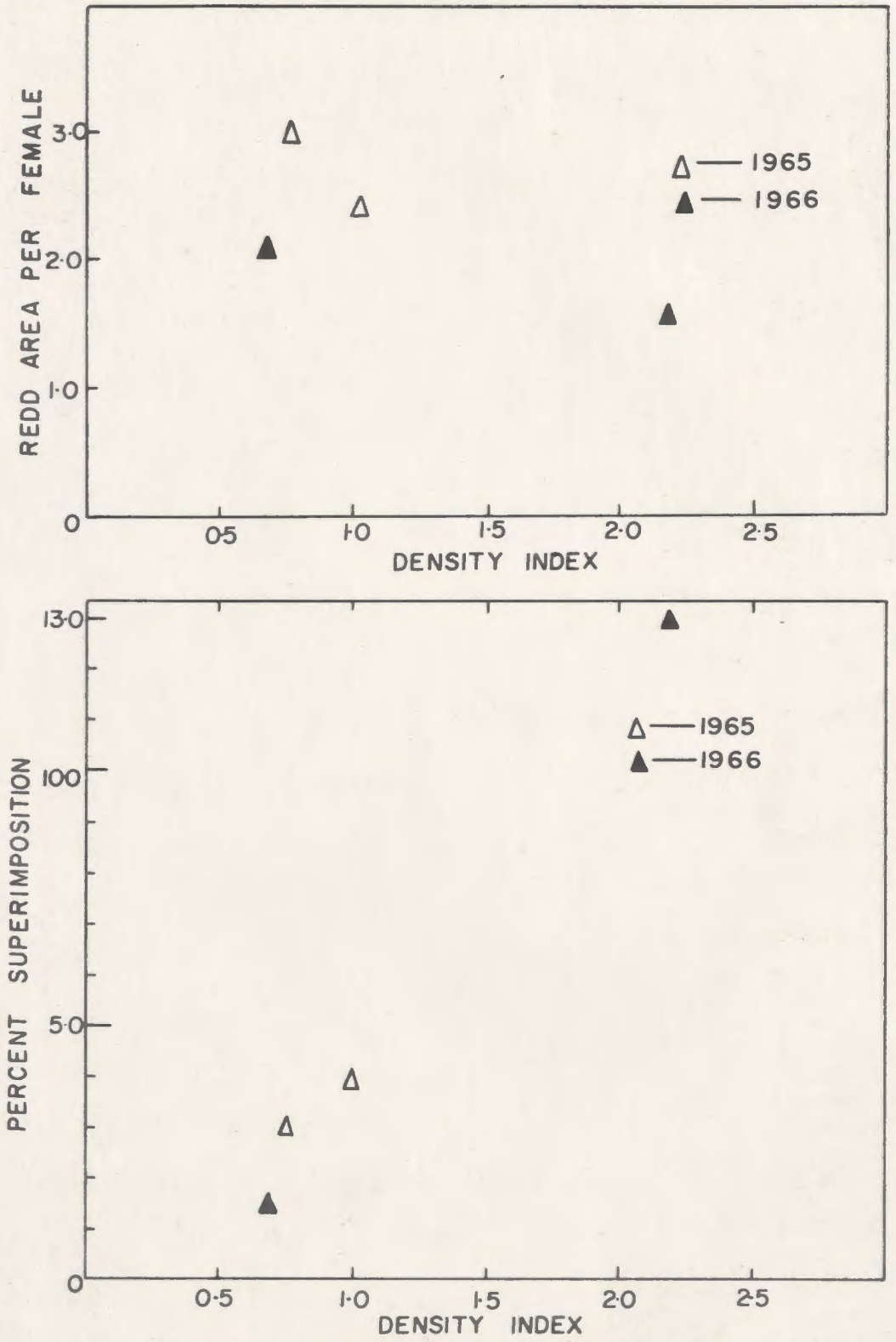


Fig. 27. Redd area per female and percentage redd superimposition related to spawning density, Indian River Spawning Channel, 1965, 1966.

Table IX. Spawning density, redd size and redd superimposition, Indian River Channel, 1965, 1966.

Year	Density Index	Redd area $(yd)^2$ per redd	Redd area $(yd)^2$ per female	Percent of available spawning area utilized	Percent of redd area superimposed
1965	1.00	2.01	2.48	17.66	3.89
	0.77	2.28	2.99	16.00	3.01
1966	2.19	1.46	1.62	25.26	13.10
	0.69	1.62	2.08	11.37	1.43

factor tends to fall substantially below 2 square yards. Annual variation is also apparent in the redd area data. In the low density sections, the area placed in each redd or the average redd area utilized per female was of higher magnitude in 1965 than in 1966 for either datum. It can also be seen from these average figures, that area per redd in all cases tends to be less than redd area deposited per female. This indicates that some females must on the average be responsible for placing more area into nests than that represented by one of these so-called redds. Actually, in both years, in any section, the number of redds plotted more closely approximated the total number of spawners rather than the total number of females.

Using the same "D.I." criteria of density, superimposition of redd areas is negligible at some level below 4 per cent when spawning concentration is light (D.I.<1), but becomes notable at the higher density (D.I.>2), increasing to over 13 per cent despite the compensating effect of reduced area in redd formation (Table IX, Fig. 27).

Annual variation can also be detected for this aspect when examining the low density sections.

McNeil (1964) from a study of Pacific pink salmon spawning beds in two Alaska streams found that egg loss and mortality increased as the density of female spawners increased and that this mortality was mainly caused by the superimposition of redds. At Indian River, egg loss from this cause was frequently witnessed; but it is quite conceivable that some redds in the channel may be partially rather than totally superimposed with much of the "overlap" being of minor consequence to egg loss and mortality. For this reason, the redd area superimposed was classified as "critical" or "marginal" to egg survival dependent on whether superimposition involved just the borders of the redds or also included at least some of the central portions where egg nests were largely located (Fig. 20, Pen A, 1965). This examination indicated that 90 per cent of all cases had some critical overlap with the exception of the low density section of 1966 which had 80 per cent with some critical overlap.

Table X. Assessment of fry progeny from 1966 spawning escapement, Indian River Channel, 1967.

	High Density Sections (D.I. = 2.19)	Low Density Sections (D.I. = 0.69)
No. fry estimated	48,116	40,441
No. fry per pound of female fish spawning	276	278

The increase in redd area superimposed in the highly populated spawning regions and the suspected associated physical damage to eggs does not seem to be reflected in counts of fry progeny which resulted with

hatching the following Spring. According to Table X, in 1967, the number of fry produced per pound of female spawning in either high or low density sections were similar suggesting that the higher superimposition at the higher spawning density was not very critical.

However, there is an additional factor connected with gravel cleaning which complicates this evaluation. The practice of periodically cleaning channel spawning gravel with gravel screening and washing machinery every few years is thought to be quite important in improving the incubation efficiency of spawning beds because it removes fines and silt which accumulate in the gravel with time. This has been well documented in a Pacific Pink salmon spawning channel located on Jones Creek, British Columbia (Mackinnon, et al, 1961) where the highest egg to fry survival rates were recorded just after cleaning the gravel. The removal, screening, washing and replacement of gravel in 1965 just prior to the 1965 spawning at Indian River appears to have resulted in similar effective improvements in survival rates over previous years as shown in Table XI. Unfortunately, for fiscal reasons, the cleaning in that year was restricted to the upper two thirds of the channel, and was not completed in the lower portion until 1967. This meant that in 1966, all redds in Sections II and III were placed in material previously cleaned but that 70 per cent of the total redds further downstream in Section IV (the low density section), were placed in material which was not cleaned. One would reason from this that had spawning density been held constant in all sections, the advantage afforded egg incubation from gravel cleaning in Section II and III over Section IV would have been greater resulting in a higher fry output per pound of female in the upper two sections. However, at the densities that prevailed, the outputs obtained

were about the same. This leads one to surmise that the higher spawning densities with higher redd superimpositions in Sections II and III were effective in reducing the fry output.

Table XI. Egg deposition and fry survival, Indian River Spawning Channel, 1963 - 1966.

Spawning Year	Channel egg deposition*	Fry produced	Egg to fry survival (percent)
1963	161,875	46,000	28.4
1964	450,625	168,000	37.3
1965	234,500	150,000	64.0
1966	192,500	90,000	46.8

* Based on 700 eggs per lb. of female fish.

In Table IX as spawning density increases, the proportion of spawning ground utilized increases despite the corresponding redd area per female decrease. The proportion of spawning ground utilized increases from 11 per cent at the lowest density index to 25 per cent at the highest density index. Hence, one sees that at a prevailing density of one female per 6.4 yards or 1 fish per 5 square yards (D.I. = 2.10), roughly one quarter of the available area following spawning has been placed in redds.

Burner (1951), in his work with chinook, coho, chum and sockeye salmon (genus Oncorhynchus) in the Lower Columbia River System, recognized the necessity for a large amount of space between redds. He suggests for these species that the average redd size should be multiplied by four to determine the average space required by a spawning pair. Stuart (1960) dealing with

trout, also recognized the need for a large inter-redd space. He allowed seven to eight times the redd area in calculating the trout capacity of an artificial spawning ground. According to these investigators, a prevailing density of 6 or 7 yards per female salmon is approaching the practical capacity of Indian River Channel if one assumes these generalisations for trout and Pacific salmon apply to Atlantic salmon.

McNeil (1967) has advanced three general hypothesis that may be used to describe the distribution of redds within a spawning area:

(1) hypothesis of uniform dispersion - once a redd has been dug, there is decreased probability of further digging at the same location.

(2) hypothesis of random dispersion - redds are dug at random locations.

(3) hypothesis of contagious dispersion - once a redd has been dug there is increased likelihood of re-digging at this location.

For the most part, results of the Poisson and Negative Binomial analysis at Indian River support the second hypothesis with some tendencies leaning to the third. However, certain qualifications must be made. One should be reminded that for these analyses, "redd" was defined as merely a spatial entity of increments and that the first increment in the redd was taken as the location of each redd within each section for each year. However, it was also previously indicated that redds built over a period of two or three weeks probably contained a series of successive increments belonging to each of several different females. This means that, in certain cases, if a redd was re-defined as "the successive workings of

one specific female", then where one redd was previously located for the analysis, up to possibly three could now be classified, all contiguous and within the same vicinity of bed length. This undoubtedly would increase the degree of redd clumping over that reported since more redds would be classified adjacent each other. However, it would be impossible to apply such a definition and classification at Indian River which requires reclassifying the "redd" based on datings of increments within it because as previously noted, one female is sometimes replaced by another without any time gap between series being noted. Unless all fish in the channel had been tagged and all the increments have been alotted to specific females, such a definition could not be intelligently used in the analysis. Hence, the definition of redd, if more specific, might indicate an even greater degree of contagion in the distributions but this classification is impossible to implement in the field with the facilities available.

While there may be an apparent contagious element unaccounted for in the redd distributions at Indian River, because of a generalized definition of the redd, in another sense, the attachment of nests by different females upstream of previous nests in a redd represents a uniform element. This phenomenon probably results in less superimposition of egg nests than if females dig in altogether new area. If a female elected to add to a former redd, she would start upstream of the last digging largely avoiding any overlap of digging which could be critical to previously laid eggs. If, on the other hand, a female begins digging in a new area, the incidence of serious nest overlaps may occur especially at high spawning densities because the building of nests in new area is

probably more a random or contagious phenomenon than a uniform one (McNeil, 1967, 1964). A further circumstance which may attribute to a uniform distribution is the apparent small amount of upstream-downstream overlap. Very few instances occurred where redds downstream tended to increase significantly upstream beyond the first increment of another redd whether this redd upstream was in the process of being built and possibly defended by a resident pair, or whether this redd was completed and abandoned at an earlier date. Sometimes, there is even evidence to suggest that if the downstream redd does not terminate but continues upstream, it may be built into vacant ground on the left or right of the upstream redd.

On the other hand, in certain years the Chi square analysis detected uneven utilization of bed between channel spawning areas and between channel sections of width. Certainly, these cases do not indicate significant localized redd clumping as isolated with the Poisson and Negative Binomial analysis about the rock weir in 1965. Rather, the unevenness detected is more a manifestation of change in utilization throughout entire portions of the channel examined since it occurs to the same extent in each individual quadrat.

In retrospect, it appears that the redd distributions at Indian River mainly conform to a hypothesis of random dispersion at the spawning densities examined. Certainly, this is a generalization since both contagious and uniform elements appear to exist in the distributions along with spatial changes in the utilization from area to area and from edge to center of the channel. Moreover, one notable case of contagion was detected on a spawning area which may in some way be associated with

a rock weir - a possibility which will be examined further in another section. It would also appear that at spawning densities of one fish per 6 or 7 square yards, a capacity level is being approached in the channel where serious superimposition is probably still minimal but could become important at higher densities.

B. Physical Aspects of Spawning Distribution

1. Water Temperature, Light and Precipitation

Observations on spawning salmon during the early part of the 1965 season suggested that daily fluctuations in water temperature might possibly relate to the number of spawners observed to move onto the spawning areas during each of the four daily spawning counts. Upon plotting the temperature-activity relationships as time series for each year, a seasonal trend was indicated with large daily fluctuations about the trend and this was accounted for by the fitted polynomial curves.

Figs. 28 and 29 illustrate the 1965 and 1966 midnight temperature and activity series treated in this way. In 1965, spawning activity observations did not commence until the end of the first week of spawning accounting for the high readings of activity plotted at the beginning of the series. Since two dissimilar spawning densities were maintained in 1966, activity was examined separately within high and low density sections.

Fitted water temperature and activity curves have accounted for trend with time (whatever its cause), so that the residual variance (represented by the departures of the observed points from the trend lines in the figures) may be correlated independent of time. For both years, all daybreak and afternoon paired readings were placed in a "daytime"

group and all evening and midnight paired readings were placed in a "night time" group. This combining of day and night periods was considered necessary on the basis of the few paired readings available for some periods (e.g. N as low as 11 for 1965 afternoon period). This treatment of the data resulted in the computation of two correlation coefficients for 1965 and four coefficients for 1966 as shown in Table XII.

For the 1965 data, correlation coefficients for both daytime and night time categories were significant (Table XII). A somewhat higher correlation coefficient was obtained for the dark than for the daylight group. Water temperature accounted for better than one quarter of the total daytime variation and for one third of the total night time variation. However, coefficients for the 1966 season were not very high, none being significant at the 0.05 level. Except for the daytime low density category, the variation accounted for was negligible.

Table XII. Summary of temperature-activity correlation analysis, Indian River Spawning Channel, 1965, 1966.

Year	Period	Spawning density	Correlation coefficient (r)	Significance of r from zero		Percent of total variation
1965	Daytime	Low	0.512	sign.	.05>p>.02	26.0
	Night time	Low	0.577	sign.	p>.01	33.0
1966	Daytime	Low	0.301	nonsign.	0.1>p>0.05	9.0
		High	0.149	nonsign.	0.4>p>0.3	2.2
	Night time	High	0.132	nonsign.	0.5>p>0.4	1.7
		Low	0.124	nonsign.	0.5>p>0.4	1.5

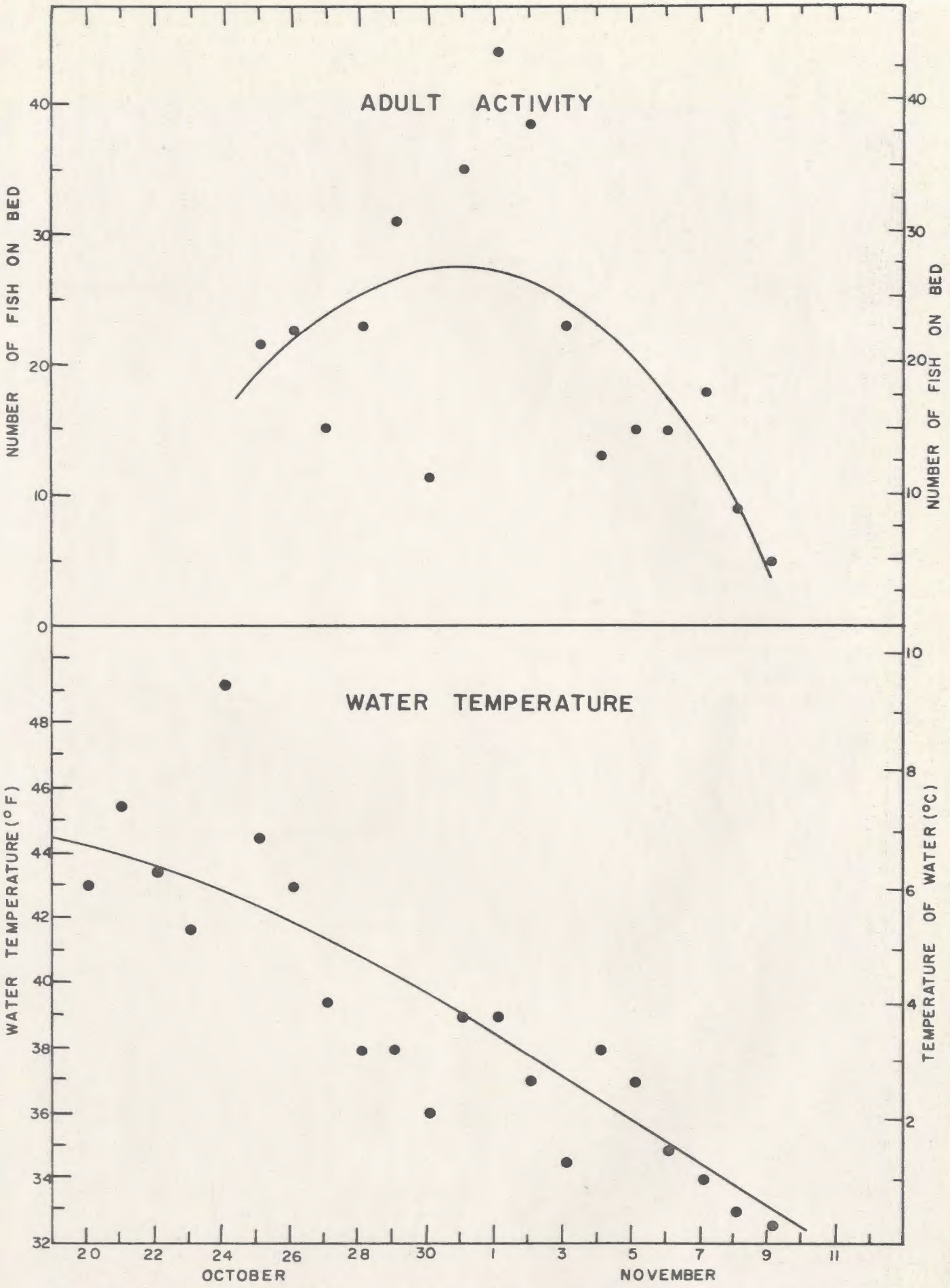


Fig. 28. Daily fluctuations in water temperature, compared to daily fluctuations in adult activity, with polynomial curves fitted, Indian River Spawning Channel, midnight period, 1965.

The most notable coefficients for any year or period mainly occur in the sections kept at low spawning density. All spawning in 1965 was at relatively low density while one low density section in 1966 had the highest association for either of the daytime or night time categories. One would suspect that any manifestations of water temperature at higher spawning densities could be masked by some overriding effect such as less space or territory for spawning. At least, the example in Fig. 29 indicates that adult activity may be altered by smaller space allotments since the peak in the high density section during the midnight period of 1966 occurred four days later than in the low density section. However, that view is disputed to some extent by the three lesser coefficients. Here, the lowest coefficient recorded was in a low density section while the other two coefficients for high density were somewhat higher. Further discrepancies are evident in the data if one compares inter-year and intra-year differences in relationships. The highest coefficient in 1965 occurred at night while in 1966, the highest coefficient occurred at the same comparatively low spawning density during the day. Moreover, the highest 1966 coefficient within high density categories occurred during the day. Hence, it is very difficult to determine how water temperature and spawning activity on the beds are related on the basis of spawning density or period of the day.

The resulting relationships may be connected more so to other things such as inter-year changes in water temperature trends or regimes. Figs. 30, 31, and 32 show fitted curves of water temperature during each of the four periods, fitted curves of adult activity in numbers of fish

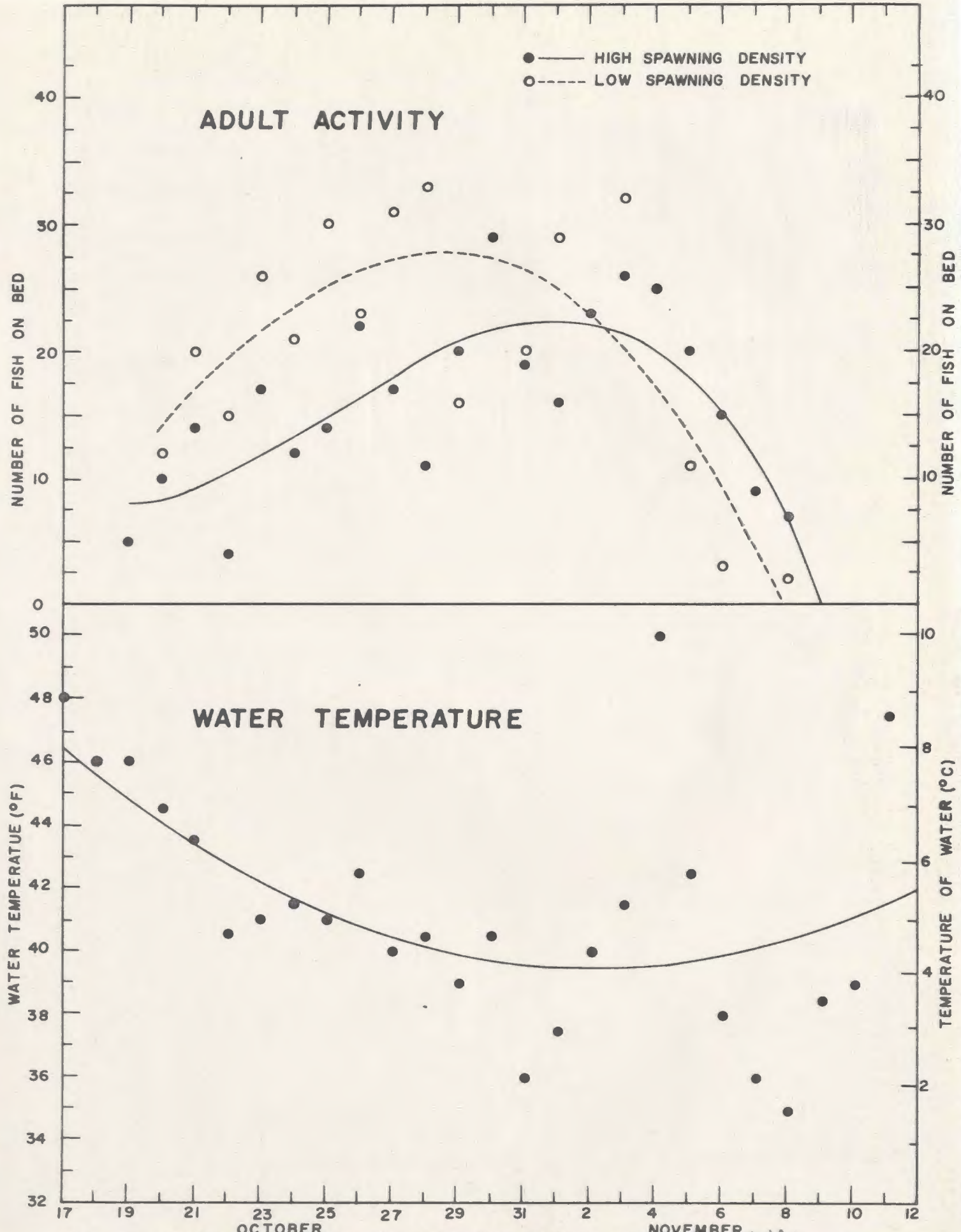


Fig. 29. Daily fluctuations in water temperature compared to daily fluctuations in adult activity with polynomial curves fitted, low and high spawning density sections, Indian River Channel, 1966.

for each of the four same periods, plus a histogram of daily redd activity expressed in square yards of ground. In each figure, the trend lines for the evening and daybreak periods closely conform to smoothed daily maximum and minimum daily water temperatures respectively. From the figures, it is apparent that the water temperature trend during the latter half of the 1966 spawning season was the inverse of that in 1965 while the regime was also much wider in the last part of 1966 than during the same interval in 1965. In 1965, (Fig. 30), start of spawning (as indicated by the commencement of redd activity) was coincident with a mean daily water temperature regime of 43.5°F - 46.5°F which decreased to average 39°F - 41°F daily during peak spawning and then decreased to 32.5°F - 33.5°F by the end of the season. During 1966, (Figs. 31 or 32), the first redd building began between 43.5°F - 46°F, decreased also to average 38°F - 41°F by mid-season but then increased greatly to finally average 40°F - 42°F at the very end of the season with the regime just prior to season's end much accentuated over that which occurred in 1965. A closer inspection of the actual differences in daily maximum and minimum temperatures averaged for each of three periods is shown in Table XIII. While the actual daily

Table XIII. Average daily fluctuations in water temperature for various periods prior to end during spawning, Indian River Channel, 1965, 1966.

Period	Average daily fluctuations °F	
	1965	1966
Sept. 25 - Oct. 15	4.1	3.9
Oct. 16 - Oct. 29	4.2	3.3
Oct. 30 - Nov. 12	2.7	7.2

regime averaged less than one degree temperature difference in the period before spawning or during the first half of spawning for either year, the daily degree fluctuations are seen to be almost three times as great in 1966 for the latter half of spawning.

It was wondered if the low 1966 correlations could be connected with the changes in water temperature trend and regime that occurred in 1966. Inspection of the paired deviations for fish activity and water temperature showed that positive associations were just as marked and frequent (or even more so) in the latter part of the spawning season as in the first part for any period of the day. In a further attempt to account for the low 1966 coefficients, the water temperature trends in the three week period just prior to spawning were also compared for each year. However, trends for both 1965 and 1966 data appear very similar during this period along with the water temperature extremes composing the maximum-minimum values. The lowest daily water temperature recorded within this period was in 1965, while the highest temperature occurred in 1966 but, in both cases, the extremes only exceeded recorded points within the compared year by 1.5°F.

When examining Figs. 30, 31, and 32, one can see a relationship between adult activity expressed in numbers of spawners on the beds and redd activity expressed in terms of redd area per square yard. It appears that redd building for the first part of any season must be largely attributed to night time activity as reflected by the evening and midnight observations. All periods of the day contributed during the peak and during the latter part of the season whether the annual trend of water temperature was decreasing or increasing. Peak of daybreak, afternoon,

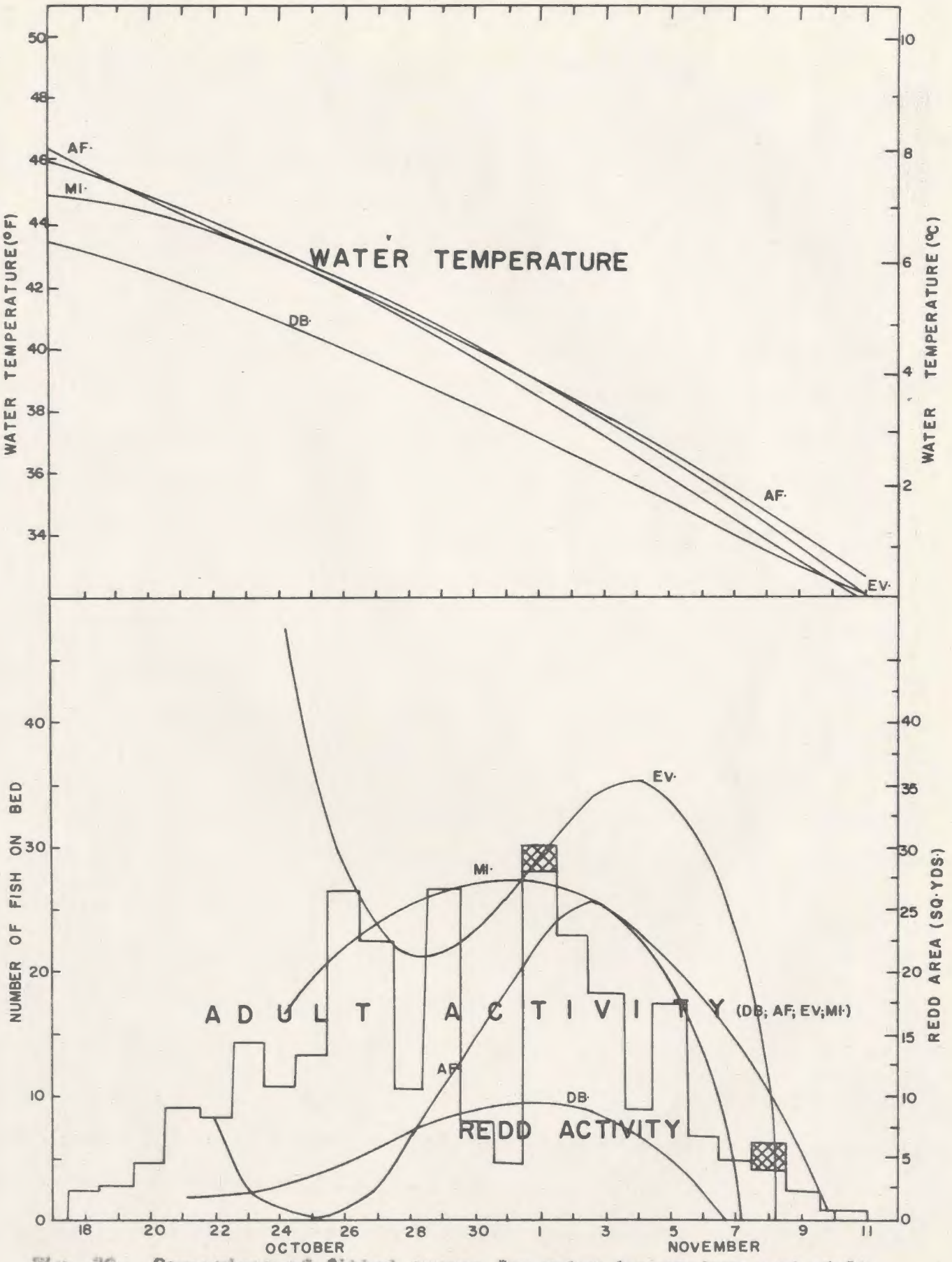


Fig. 30. Comparison of fitted curves for water temperature and adult activity by daily period (denoted by abbreviation) along with histogram of actual redd area built on beds, Indian River Channel, 1965.

and midnight activity coincided fairly closely with modal redd building but the peak for the evening period, if well defined, was usually later than the mode for redd building.

A small amount of spawning during the latter half of each season in the evening and around midnight was not true redd activity. As indicated by cross-hatching in Fig. 30 and Fig. 32 some redd area placed in the channel on November 1 and 8, 1965, and on November 3, 1966, contained no eggs. But post spawn activity in the form of false redd building was negligible. Nonetheless, it is possible that in 1966, some adult activity at this time was discharged in defence of old redd territory. In the low density section (Fig. 32), evening activity must have persisted until the end of the season and possibly longer. At least, this seems possible in view of the large number of fish frequenting the spawning areas as late as November 8. On the other hand, in the high density sections, (Fig. 31), the activity curves fell short of some of the true redd activity. This was attributed mainly to the fact that adult activity observations ceased November 8, while redd plottings continued the remaining few days of the season. Hence, it appears that post spawning activity in most cases was very low. As previously mentioned, trial redd activity often begins long before actual spawning commences. Frequently trial redds start as early as September and continue mostly at night. Counts of adult activity during 1965 did not commence until several days after the beginning of true redd building so the trend equations (Appendix Table VII) could not be used to describe the left tail of the curves. However, during 1966, in both low and high density sections, (Figs. 32, 31), one can see that the unplotted extreme left tails of curves representing night time periods possibly do not commence with the first true redd building in this year.

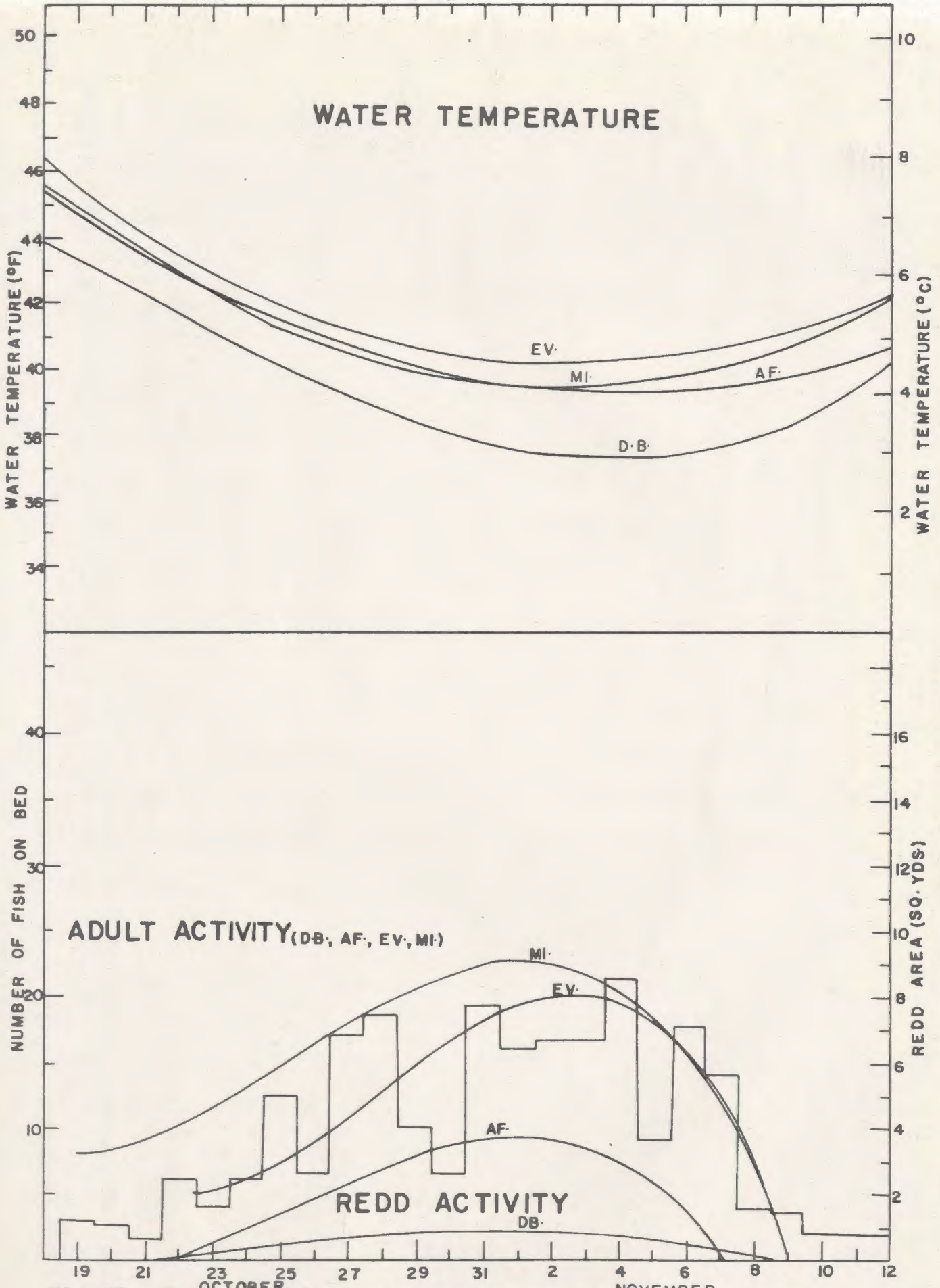


Fig. 31. Comparison of fitted curves for water temperature and adult activity by daily period (denoted by abbreviations) along with histogram of actual redd area built on beds, high spawning density sections, Indian River Channel, 1966.

It is interesting to note that the daybreak period with the lowest prevailing daily water temperatures also had the lowest corresponding count of spawners composing the trend for the same period. However, the other three periods in Figs. 30 to 32 do not indicate the same marked pattern where proportionately higher prevailing water temperatures within a period are associated with proportionately higher counts for the same period. As an example of day to day values, Table XIV presents two days of actual counts in 1965, when one further early morning count was made in addition to the regular ones each day. Unfortunately, the daybreak (0730 hrs.) check was missed on October 28, but on October 29 it was made and, as expected, it had the lowest water temperature and lowest activity recorded for that day. However, a morning dark count at 0600 hrs., with the same low water temperature, exhibited a very much higher count of spawners on the beds. Another discrepancy exists between the evening and midnight period on this date. Referring back to October 28, an early morning dark check (0300 hrs.) and an afternoon check with identical water temperatures resulted in quite different counts.

Table XIV. Water temperature and spawning counts, Indian River Channel, 1965.

Time	October 28		October 29	
	Temp. °F	Number	Temp. °F	Number
0300	37	11		
0600			34	17
0730	35	n.r.	34	5
1600 - 1700	37	3	35	6
2000	37	24	36.5	22
2400	36	22	36.0	31

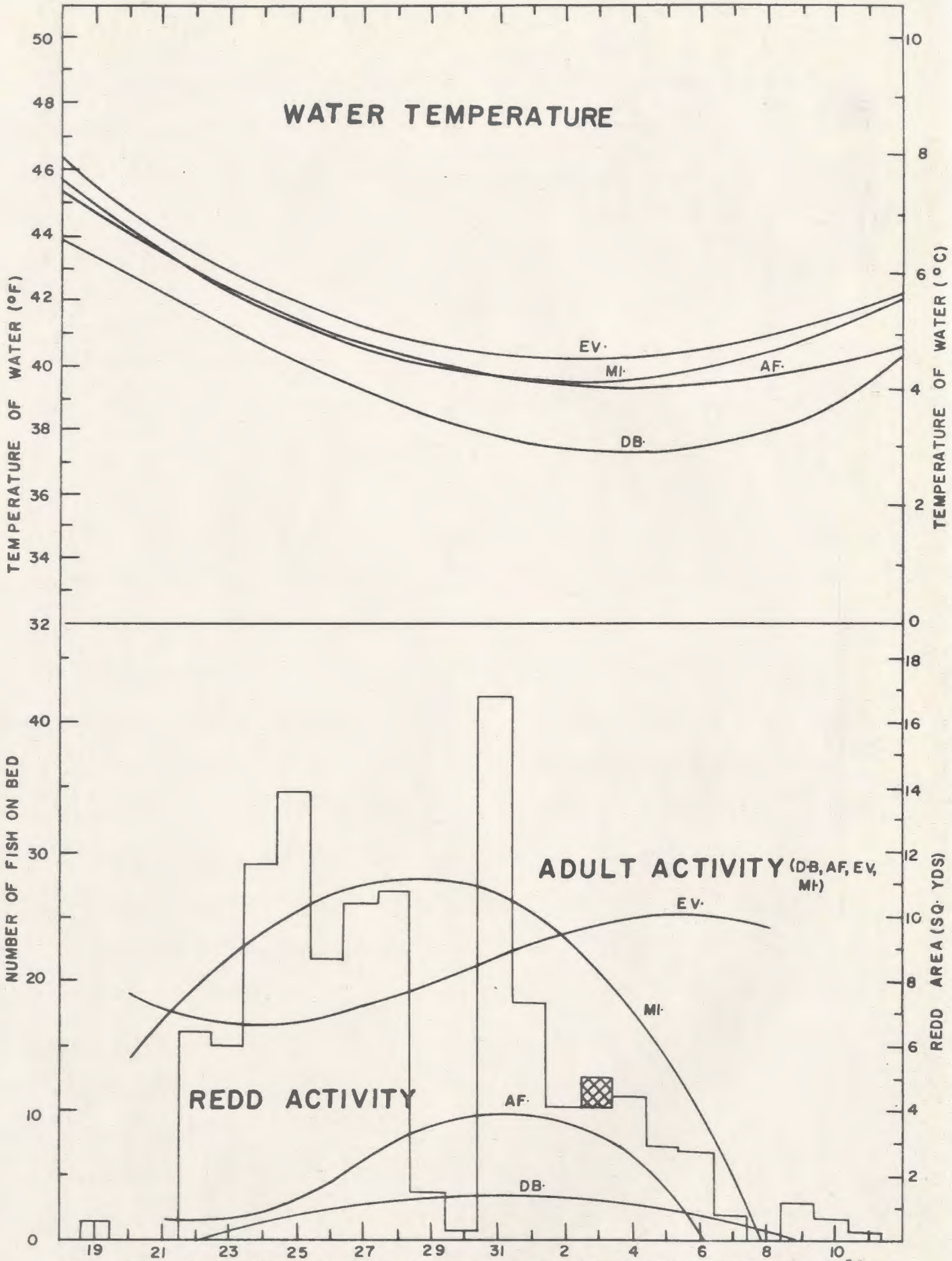


Fig. 32. Comparison of fitted curves for water temperature and adult activity by daily period (denoted by abbreviations) along with histogram of actual redd area built on beds, low spawning density section, Indian River Channel, 1966.

The above examples indicate that light may be another factor related to spawning activity. The low 1965 and 1966 correlation coefficients for water temperature and activity show that other environmental factors may be responsible for some of the activity variation not accounted for by water temperature. Even the discrepancy between evening and midnight counts of October 29, may be connected with light intensity since this was an overcast day which was clearing by early evening.

For Atlantic salmon spawning, no comprehensive studies were noted in the literature which described the relation of daily water temperature or light to actual spawning. Jones and King (1949) did note that spawning occurred in the tanks between 36°F and 42°F, and in an adjacent river at temperatures between 36°F and 47°F. They also observed that spawning fish did not seem affected by bright artificial light. Fish that were not engaged in spawning would not move to the spawning bed of the observation chamber until the light was extinguished; but the writers admit that these nonspawning fish might have remained moreso in the pools anyway.

In other species, Fabricius and Gustafson (1953) during aquarium spawning studies of Arctic char (Salvelinus alpinus), came to the conclusion that water temperature, although affecting the time of gonad ripening and the period of migration to spawning grounds, probably does not exert any great influence once spawning begins in the species but admit that fluctuating water temperatures during spawning may be of some minor importance. In their observations on light, they found that spawning mainly occurred during daylight. Spawning only occurred at night if electric lights were switched on. However, from similar observations

on spawning grayling (Thymallus thymallus L.), they believe that the daily rhythm of water temperature is the most important of the stimulii affecting the timing of the rhythm of spawning and territorial defense (Fabricius and Gustafson, 1954). Rising temperature during the day seemed to stimulate these activities together with spawning migration; but, Gustafson (1948) found that the most intense migration took place between 1600 hours and midnight at a time when water temperature was falling. He, therefore, considers light may also stimulate the defense of territories and the spawning but temporarily inhibit migration in the grayling. Hence, it appears that daily changes in water temperature and light usually play an important but varying role from species to species during spawning.

An attempt was made to examine precipitation in relation to spawning activity. For what readings were available, rainfall showed a consistent positive relation to adult activity for the two years during afternoon periods but only when spawning density was low. Snowfall was found to relate in a positive manner with activity during afternoon periods but during 1966, only in the high density section. However, this interpretation of precipitation is considered of little value because of the low frequency in occurrence.

From the foregoing examination of water temperature, light and precipitation, daily fluctuation in water temperature and light appeared the most accountable for some of the daily changes that occurred in numbers of fish moving from the holding pools to the spawning areas. The degree of relationship between temperature and spawning activity was measured as changing from year to year - a phenomenon which is difficult

to explain. Very little can be postulated on light since it could not be recorded objectively throughout the day as was water temperature since the necessary instrumentation was not available. The further recording of light intensity with a special underwater photometer placed right in the channel would be necessary to confidently relate this factor to adult activity. The occurrence of rainfall and snowfall during the two years of observations is considered insufficient to even form a hypothesis about either factor.

2. Water Depth and Velocity

Depth and velocity spawning preferences were examined with space and time.

In 1965, mean depth and velocity preferences for tagged fish in Section II were compared to the same preferences for untagged fish in Section III where spawning density was somewhat higher. No significant difference was measured between them indicating preference must have remained similar in both areas despite the marking and slight density difference (Table XV). Because of this homogeneity in redd depth and velocity preferences, these two groups of fish were combined into one channel population in the following examination of depth and velocity.

Table XV. Velocity and depth preferences during redd construction, at water flow of 18 cfs., Indian River Channel, 1965.

Section	N	Velocity f.p.s.				Depth (ft.)			
		Range	Mean	S.D.	t-test	Range	Mean	S.D.	t-test
II (tagged)	20	0.9-2.1	1.495	0.338	.05 level (non sign)	0.5-1.4	0.745	0.214	.05 level (non sign)
III	114	0.5-2.7	1.263	0.378		0.5-2.1	0.841	0.246	
II & III	134	0.5-2.7	1.305	0.383		0.5-2.1	0.827	0.244	

The means and regime of velocity and depth preferences during redd building are given for this composite sample in Table XV (Section II and III). These spawning preferences are compared to the measurements of water velocity and depth conducted on Spawning Areas One and Four of the channel. The data is presented in Fig. 33.

Frequencies correspond closely despite the fact that availability curves were established only on readings from two spawning areas, while preferred curves are based on water depth and velocity selections recorded for fish building on all six spawning areas. This correspondence of frequencies is a further indication that fish have distributed themselves spatially over channel spawning areas making full use of the depth and velocity profiles provided.

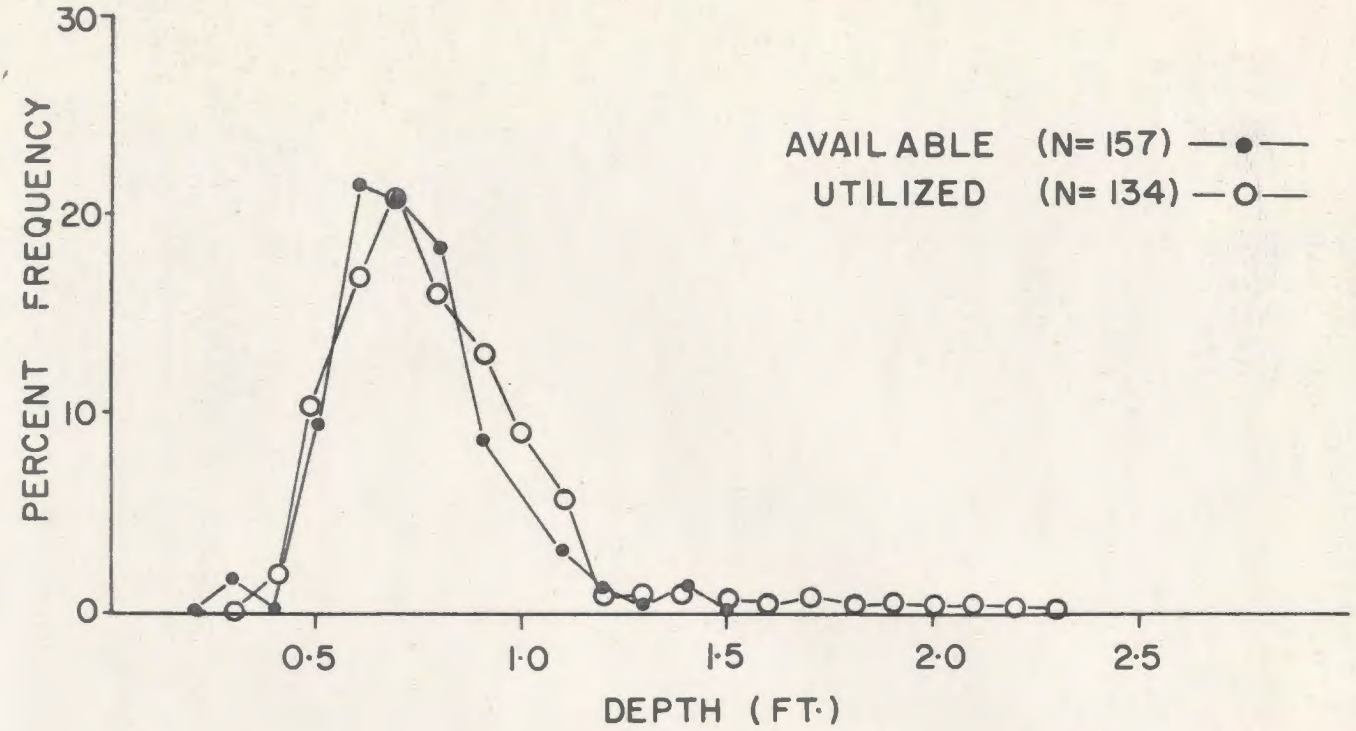
In 1966, velocity and depth preferences were compared between tagged and untagged fish separated in Sections II and III at the high spawning density and the untagged faction of the population separated in Section IV at the much lighter density. In Sections II and III inclusive, fish spawned at significantly higher depth and significantly lower velocity than fish in Section IV which might indicate that the differences in spawning density or marking in some way influenced the selection of spawning depth and velocity. Table XVI shows that when Section II and Section III were examined separately, tagged fish in Section II apparently spawned at significantly greater depths and at significantly lower velocities than in Section III where no tagging occurred despite the same high spawning density in each section. At the same time, it was found that no significant difference existed in preferences between high density Section III and low density Section IV where

both groups were untagged. This tends to eliminate spawning density as a possible cause of the difference in preferences leaving marking as the prime consideration. However, it will be recalled that no significant difference was measured between marked and unmarked lots of fish held at relatively similar low densities in 1965. Hence, there seems to be no consistent argument to explain the preference differences in 1966 based on spawning density differences or tagging differences.

Table XVI. Velocity and depth preferences during redd construction at water flow of 18 cfs., Indian River, 1966.

Section	Velocity f.p.s.			Depth (ft.)		
	Mean	S.D.	t-test .05 level	Mean	S.D.	t-test .05 level
II & III	0.99	0.285		1.27	0.284	
			sign			sign
IV	1.16	0.258		1.10	0.182	
II (tagged)	0.80	0.358		1.45	0.340	
			sign			sign
III (untagged)	1.12	0.285		1.21	0.258	

The difference in preference noted in Table XVI is considered more attributable to certain physical alterations which occurred in the channel bed than to any density or tagging differences. This was discovered when water discharge measurements were carried out before the 1966 spawning season. At this time, it was revealed that adjustment of the channel intake valve opening to allow channel water levels which, in 1965, gave the operational flow of 18 cfs., only yielded 13.5 cfs. This discharge



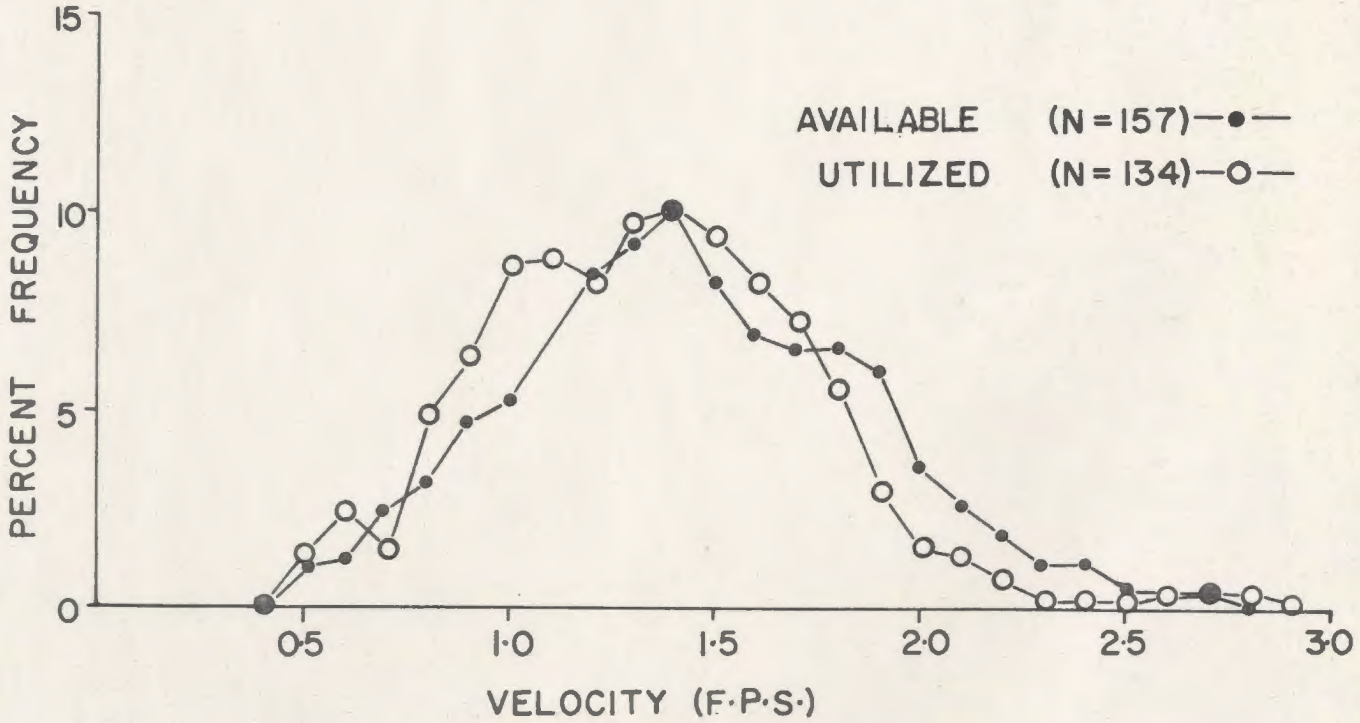


Fig. 33. Percent frequency curves for water depths and water velocities available on two spawning areas compared to percent frequency curves for water depth and water velocities utilized, Indian River Channel, 1965.

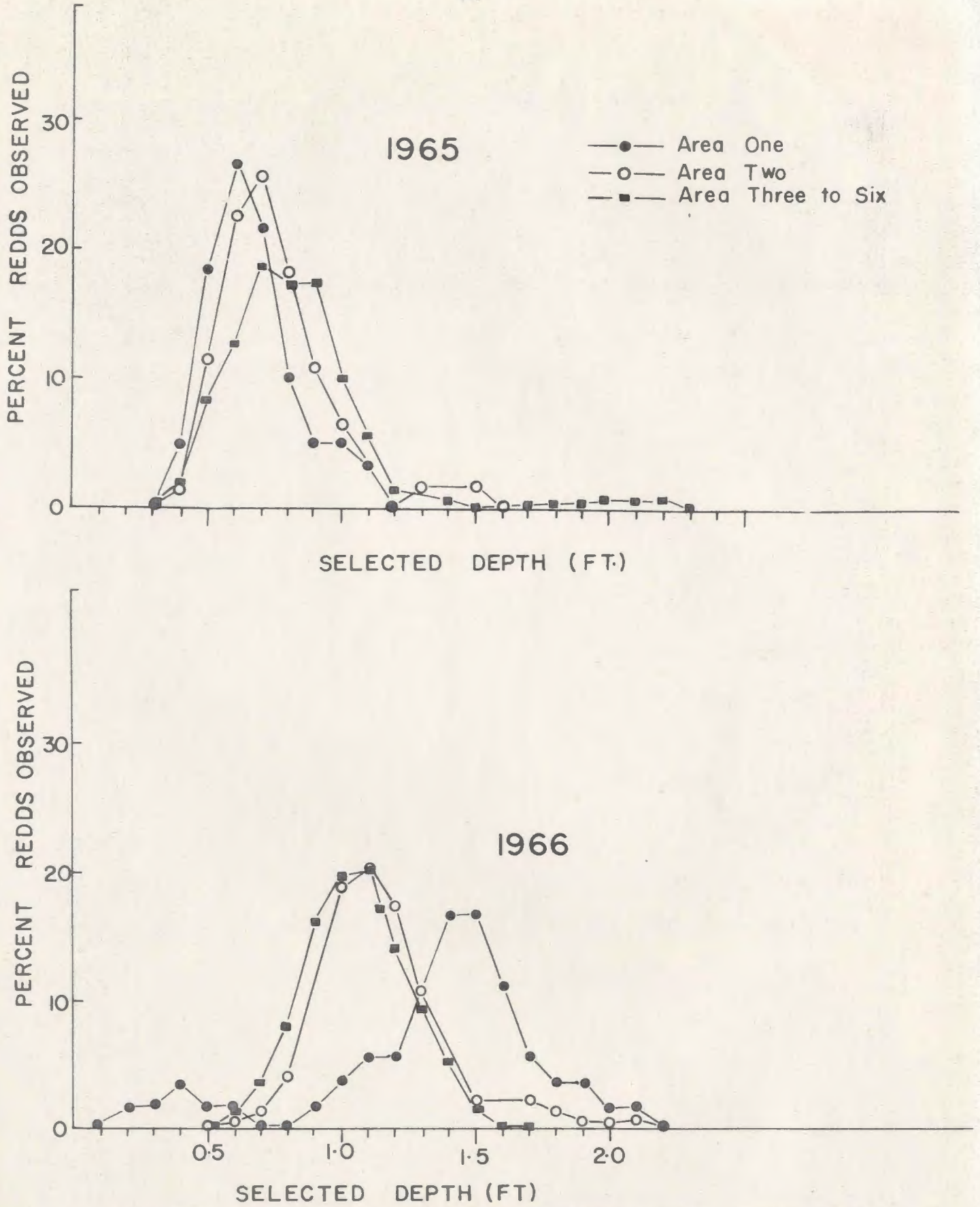


Fig. 34. Water depths selected by fish building redds, Indian River Channel, 1965, 1966.

discrepancy of over twenty percent is attributed to routine removal of silt from the channel gravel with harrow machinery prior to 1966 spawning which greatly changed the gravel bottom and bank configuration. Bringing this flow from 13.5 cfs. to 18 cfs. in 1966 has meant that the water level or water depth in the channel has had to increase with a corresponding decrease in velocity compared to 1965 profiles. In addition, it appears that fish during 1966 were confined to a section of Area One which, since 1965, contains a further alteration. Exceptional bed deepening has occurred next the edge of Holding Pool One which has increased depth and lowered velocity more so than in other areas. Also, to carry out the 1966 spawning density studies, an extra isolation fence was required below Spawning Area Two. At best, a few isolation fences are obstructed by deciduous leaf fall into the channel at this time of year, creating some back up of water upstream of the fences despite the continuous effort of one worker cleaning these barriers. However, in 1966 an additional fence, plus a somewhat higher rate of leaf fall during peak spawning, resulted in unusual back up of water.

In Areas Three to Six, where no barrier fences were present, and where only the cleaning machinery affected the flow characteristics, the selected water depth and velocity profiles were closest to those for 1965 (Figs. 34, 35). However, in Area Two, fences were also involved and the profiles differed more widely from 1965. Finally, in Area One where cleaning, isolation fences and deepening of the bed were all involved, the greatest deviations in frequencies occurred. Hence, the difference in depth and velocity between 1965 and 1966 were greatest for Spawning Area One, less for Area Two, and least for Areas Three to Six or in direct relation to the occurrence of channel irregularities described.

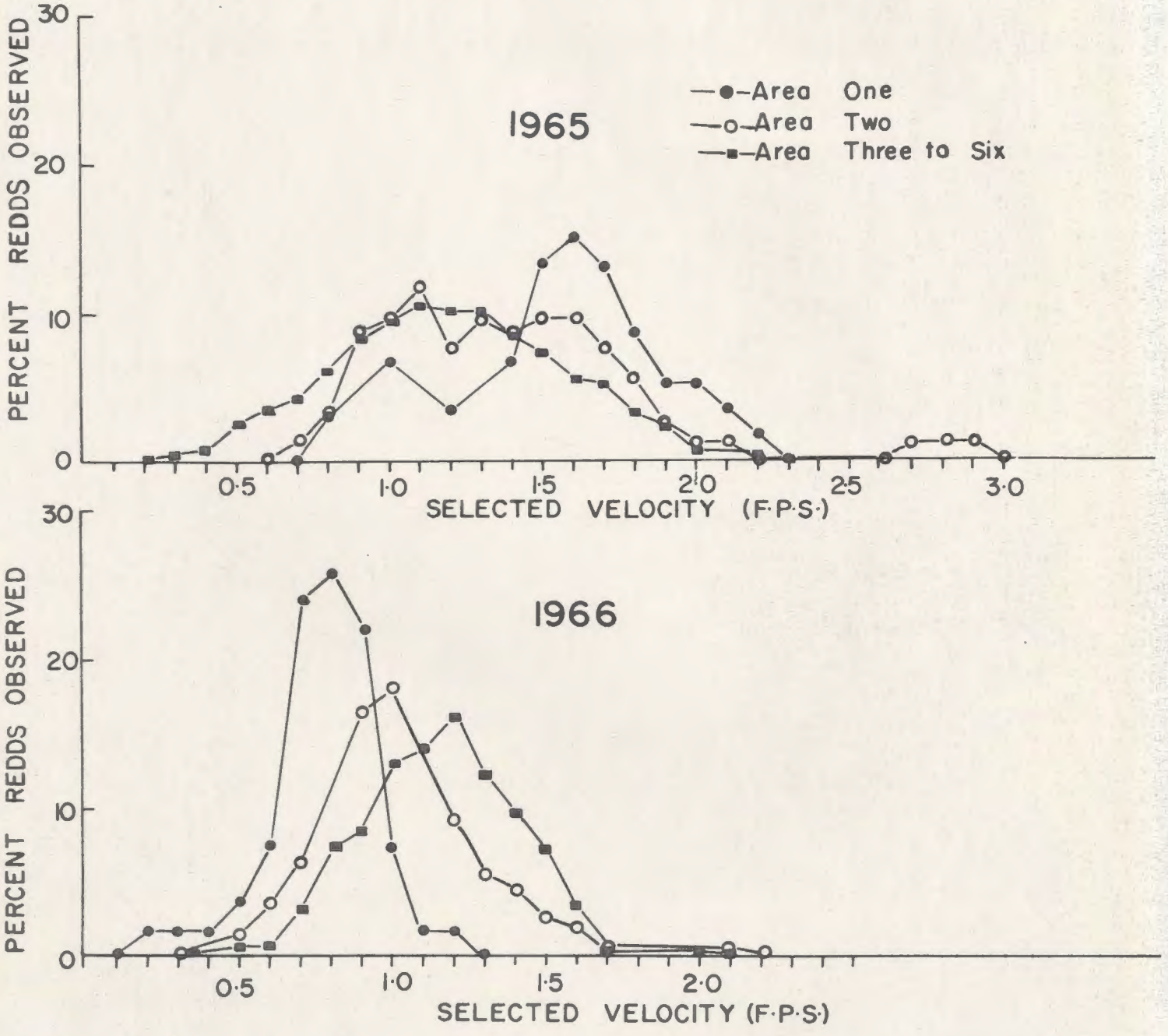


Fig. 35. Water velocities selected by fish building redds, Indian River Channel, 1965, 1966.

In spite of the inter-year changes in channel velocity and depth profiles for given discharge, fish still distributed their redd densities randomly throughout quadrats in spawning sections but tended to direct their redd building in the last year moreso to the peripheral regions of the channel in all sections. The possible connection of this edge effect to water velocity and depth preference was investigated by comparing the differences in redd preferences within peripheral and central sections during 1965 and 1966. Means and standard errors were computed for Section III (D.I. = 1.00) during 1965, for Section II plus III (D.I. = 2.16) and for Section IV (D.I. = 0.69) during 1966. The range of difference that might occur from chance at the 95% confidence level is presented in Fig. 36. The true mean is thereby established as falling within the range $\bar{x} \pm 2SE$ which is illustrated for each case. As long as "overlap" exists between ranges of central and peripheral means, no significant difference exists. If, on the other hand, no overlap was evident, a significant difference between the means was declared.

Despite the difference in redd distributions with width between 1965 and 1966, no changes in the pattern of preference in water velocity or water depth was detected in central or in peripheral regions. In both 1965 and 1966, redd water velocity preference tended to be higher at centre than along the banks while redd water depth preference was highest to the centre and left periphery. However, significant differences for corresponding width intervals between sections and between years were prevalent, the most important being the discrepancy in depth preference between 1965 and 1966. Notable differences for velocity preference between years were few and minor, the only case being the right

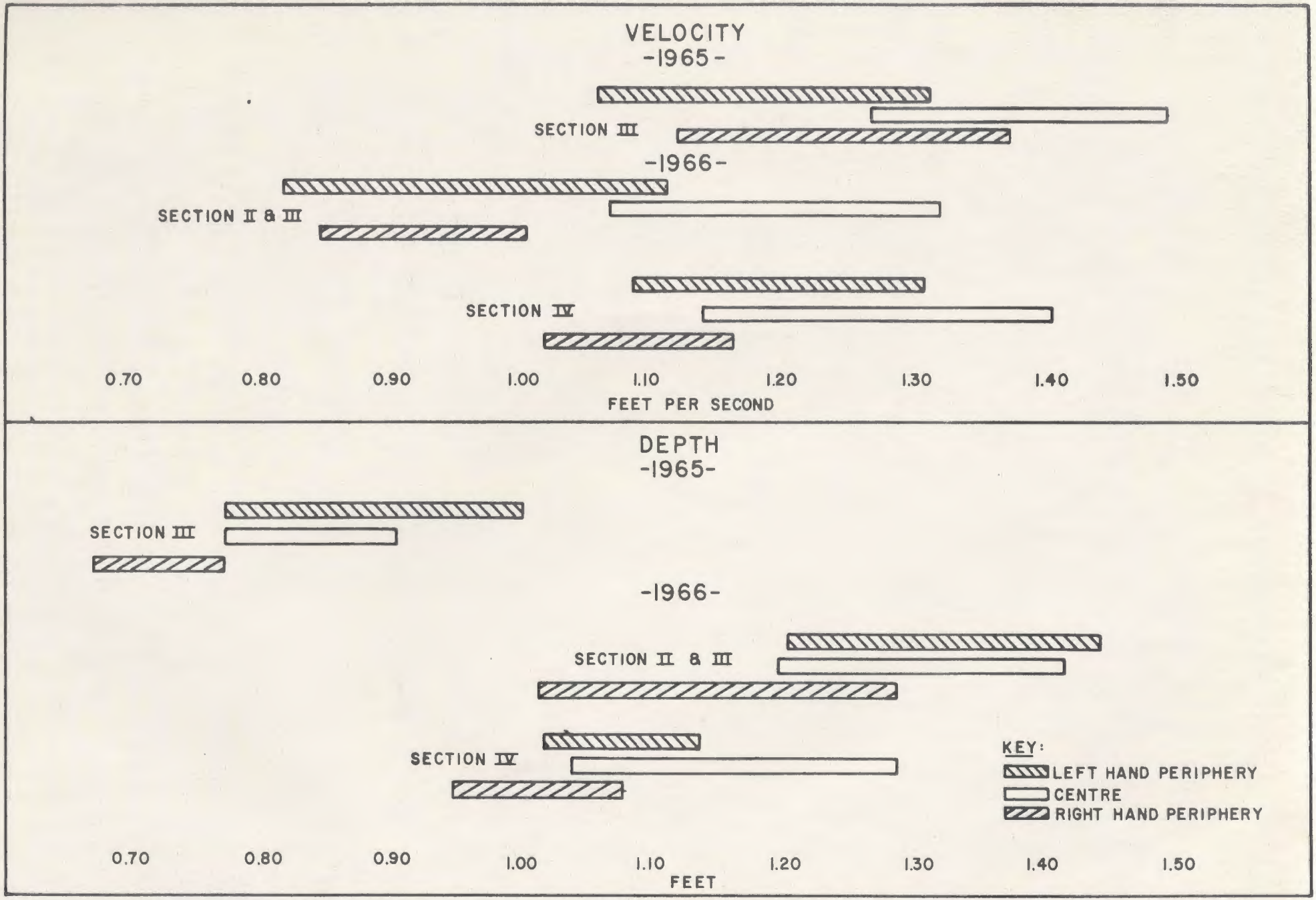


Fig. 36. Comparison of annual selections of water velocity and water depth within peripheral and central segments of channel, Indian River Channel, 1965, 1966.

bank of Section II plus III for 1966 compared to the right bank of Section IV for the same year or Section III for 1965. By comparison, depth preferences in 1966 in all width intervals of Sections II plus III and Section IV were clearly significantly higher than those in Section III for 1965.

From the very close association demonstrated in available and preference curves of 1965 (Fig. 33) and from the similarity in the annual redd distributions, it is believed that the spawning preference in 1966 also closely followed the available profiles physically altered by machinery and fences and that the increased depth preference in 1966 was due more to these alterations than to any changes occurring from spawning density, tagging or bank vegetation cover. This phenomenon of greater channel water depth availability and redd choice along the banks when examined in relation to the positioning of territories by spawning pairs provides a reasonable explanation for the higher frequency of redds along the banks. In marginal locations, members of pairs occupying their characteristic territorial positions (i.e. female adjacent one bank and male downstream and midstream to her) were afforded greater water depth in all sections and thus more vertical and horizontal space for spawning next the adjacent banks than before. This tended to allow some spawning pairs to move their territories moreso from the centre closer to one channel bank which greatly reduced the territorial expanse on the inshore side of the nests.

The "first choice" of velocity and depth was recorded for each spawning area and compared to the means for the first ten redds built on

areas (Table XVII). During 1965, the first fish to spawn in each spawning area usually chose a site with greater depth and greater velocity than the mean of the first ten preferences in the same area. However, in 1966, the relationship was not as consistent. Spawning Area One exhibited a similar trend in choice data to 1965 but the remaining areas showed a greater tendency for the first redd choice on an area to have a lower water velocity and/or water depth reading than the mean of the first ten preferences on the same area.

Depth and velocity means for the first seven days of channel spawning were also compared to the succeeding fourteen days. No consistent relationship could be established within years or between years with this treatment of the data.

Depth and velocity preferences for both 1965 and 1966 were also examined in quadrats with different integral redd densities. Again, no meaningful trends or relationships were established between water depth or water velocity preferences and redd density categories existing in quadrats.

Although available depth and velocity profiles were not collected in 1966, from the very close associations demonstrated in available and preference curves of 1965 (Fig. 32) and from the similarity in the annual redd distributions, it seems reasonable to assume that spawning preference in 1966 also closely followed the available profiles physically altered by the gravel harrowing machinery and the fences. The most plausible explanation for the building of redds more frequently along sections of channel bank in 1966 seems to lie with the physical changes which increased the water depth there. It also appears that

Table XVII. Water velocity and water depth preference of the first redd located on each spawning area compared to the mean for the first ten redds built on each spawning area, Indian River Channel, 1965, 1966.

Year	Density	Spawning Area	Velocity choice f.p.s.		Depth choice (ft.)	
			First redd.	First 10 redds.	First redd.	First 10 redds.
1965	Low, all areas	1	0.91	1.50	1.00	0.67
		2	2.04	1.38	0.60	0.68
		3	1.77	1.35	0.90	0.77
		4	1.44	1.07	0.90	0.81
		5	0.66	1.38	1.10	0.79
		6	1.16	0.99	1.31	1.01
		Average	1.33	1.28	0.97	0.79
1966	High	1	0.81	0.78	2.00	1.39
	High	2	0.91	1.01	1.00	1.20
	Low	3	1.21	1.10	0.80	1.09
	Low	4	1.17	1.29	1.20	1.14
	Low	5	1.25	1.22	1.00	1.00
	Low	6	0.77	0.98	1.00	1.10
		Average	1.02	1.02	1.17	1.12

the water depth and velocity regimes available in 1965 were as optimal for channel spawning as the altered profiles of 1966 since the distribution in both years remained random and unclumped except for Area Four in 1965. Assuredly, Atlantic salmon must exhibit some wide optimal preference range in their choice of spawning ground, but it is doubtful if any particular numerical velocity and depth range lying within the narrow ranges designed into the channel can be considered as more ideal for distribution at low and medium valve openings.

3. Test Egg Plants

A notable effect on the 1965 spawning distribution not mentioned thus far was discovered in connection with the 30 permeable egg containers placed in the channel spawning gravel to check on egg embryo development and survival over the Winter. Within a 2 to 11 day period following their burial (average time 4.3 days), 23 of the 30 baskets had redds constructed on their upstream borders. For three quarters of the egg plants to be associated with redds in this manner especially at such a low channel spawning density, was considered more than a chance occurrence. Hence, it was decided to investigate this phenomenon further during the 1966 spawning season.

Stuart (1953, 1954) has conducted research on water currents through gravel in relation to spawning brown trout (Salmo trutta). He has found by subsurface monometer studies in an experimental pool that the strongest current through gravel occurs adjacent to the apex of a gravel mound. In two separate tank experiments with mature spawning pairs of brown trout, he found they selected areas for nest

building just upstream from the apex of the gravel mound at the point of strongest subsurface flow. He has further demonstrated the occurrence of strong downward currents in this apical region of the redd by the use of dye indicators. In examining the sites of Indian River egg plants, it was noted that the spawning bed in front of the plants was not level but slightly rounded with a forward slope projecting upstream from the egg plant - the area in which new redds were begun. Based on these findings, a hypothesis evolved that an area of maximum subterranean current was created by the excavations of egg plants which were preferred by Atlantic salmon spawners over other areas without these formations.

Obviously, the best way to test this hypothesis would be to study the velocity of subsurface currents. However, tracing such currents by techniques available requires specialized field equipment and a hydraulic test flume for calibration of this equipment (Gangmark and Bakkala, 1958; Terhune, 1958; Wicket, 1954). This measurement of seepage rate can thereby become complicated, requiring extensive sampling procedures and great expense. On the other hand, Chambers, et al (1955) found that subterranean water drawn from the forward slope profile of a redd held more dissolved oxygen than samples from other parts of the redd, or from the same location prior to spawning, or from undisturbed gravel beside the redd. He also found that the amount of dissolved oxygen progressively decreased as water was drawn from deeper in the gravel both in spawned and unspawned sites. Furthermore, Coble (1961) in examining the relationship between dissolved oxygen and apparent velocity in a streambed found that when velocities were low, oxygen concentrations were expected to be low, and when they were higher, oxygen

levels were expected to be higher. The use of oxygen levels and dyes as indicators of subsurface velocity and currents in such an examination as this was therefore considered the next best alternative to measuring subsurface velocity.

The Paired Comparisons Test used to assess the reliability of reading oxygen levels directly with the oxygen metre probe inserted in the pipes rather than by removing a water sample for Modified Winkler Analysis (Table XVIII) did not indicate a significant difference between the simultaneous readings initially taken (0.7 p 0.6). Hence, the oxygen meter, after this preliminary comparison, was used exclusively for the duration of the study to measure oxygen content within the standpipes.

Figure 37 illustrates the results of systematic oxygen sampling in the spawning areas of the channel for a three-day period before, and a five-day period after the egg plants were installed. Oxygen readings of the monitor or control pipes for each cross section were plotted along with the daily water temperature readings. One plotting of daily water temperature was sufficient for all cross sections since temperature remained constant whether reading pipes associated with egg plants or reading pipes acting as controls. Generally, the monitor standpipe readings were very similar to the three standpipe readings for a particular cross section both before and after the installation of the egg plants, discrediting the hypothesis that egg plants (as indicated by intragravel oxygen) were creating stronger subsurface currents in the apical area of the mound than existed at the same location without the mound. Only in cross section 0+800 were there notable differences in the pipe readings. Here, the oxygen readings of pipes associated with

planting when compared to the readings in the control pipes exhibited significant differences following egg planting according to the Paired Comparisons Test. However, looking to other cross sections following planting, it appeared that this difference was due more to unusually low

Table XVIII. Simultaneous oxygen determinations using the Modified Winkler analysis and the oxygen meter - Indian River Spawning Channel, 1966.

Standpipe Number	Oxygen determination p.p.m.	
	Oxygen meter	Modified Winkler
1	11.4	11.8
3	12.3	12.4
5	10.4	10.2
6	11.5	11.5
8	11.6	11.7
14	10.4	9.6
31	11.1	11.8
31	12.3	12.4
32	11.8	11.7
33	11.6	11.8
38	11.5	11.5

oxygen levels in the control pipe than to exceptionally high oxygen readings in the three plant pipes. It will also be noted in all cross sections that there was a trend to increase in oxygen of standpipes associated with egg plants especially after their installation. However, there was a similar increase in the oxygen levels of control pipes within each section. From the plot of water temperature, the inverse relationship

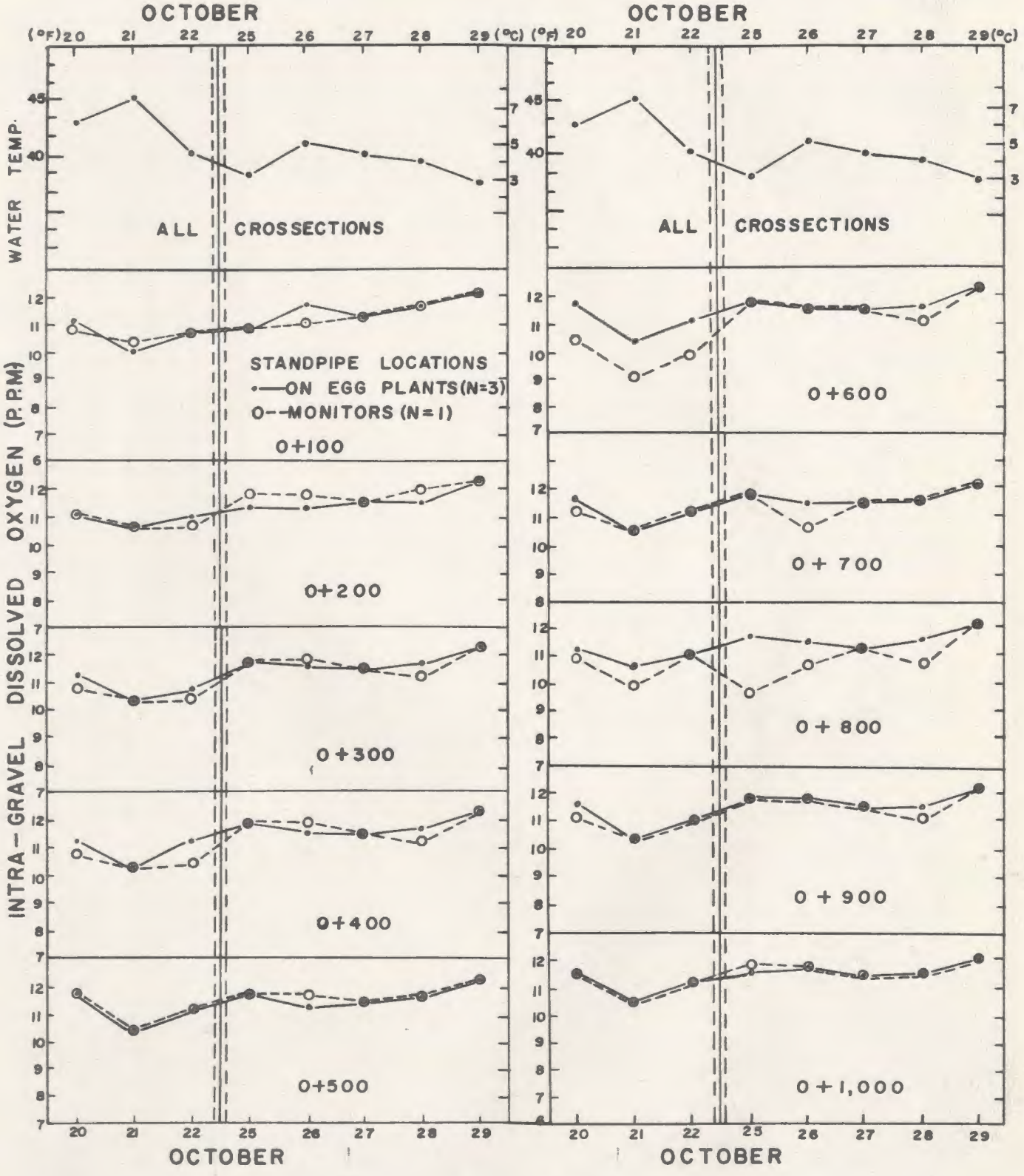


Fig. 37. Intragravel oxygen readings before and after installation of egg plants compared to readings in control or monitor pipes, Indian River Channel, 1966.

between oxygen saturation and water temperature with time was obvious. Good illustrations of this are cross sections 0 + 200, 0 + 300, 0 + 400, and 0 + 600; the remaining cross sections were also associated in this way except for two or three points in each series. Water temperature probably accounts for a large proportion of the temporal variation. Hence, it would appear that most of the long term increase in dissolved oxygen is probably associated more with decreasing water temperatures than with installing test plants.

It should also be noted that contrary to the findings of Chambers, et al (1955), dissolved oxygen levels for different parts of channel redds (Table XIX) did not vary in the manner he found. Furthermore, these variations were not detected in natural spawning areas of Indian River but some evidence of vertical gradient in oxygen content was detected in undisturbed channel area by increasing the subsurface sampling depth (Table XX). Dissolved oxygen to 10 inches bed depth illustrated no noteble change but at 16 inches, two very low readings of 3.2 and 3.3 ppm were recorded during the first two days of daily standpipe sampling. Thereafter, the oxygen content of samples increased markedly but remained 0.6 to 1.2 ppm below the values for standpipes placed in the bed at the shallower depths. It is considered that the standpipe driven to a mean depth of 16" passed through the screened gravel layer placed in the channel and penetrated an underlying layer composed of less permeable material. It is further suggested that a mechanical disturbance and/or current erosion has occurred adjacent the standpipe, resulting in an interchange between water of these two layers after the first 48 hours of sampling. The upwelling of subterranean water is

Table XIX. Oxygen levels within different regions of redds or undisturbed spawning area, of channel or river at mean sampling depth 5.5 inches - Indian River, 1966.

Date	Water Temp. °F	Channel						River	
		Redd "A"			Redd "B"		Undisturbed	Redd "A"	
		Below apex	R.b.s.	L.b.s.	Below apex	Rear Tailspill	Gravel	Apex	Undisturbed gravel
Oct. 27	40	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5
28	39	11.6	11.8	11.8	11.6	11.8	11.6	11.8	11.8
29	37	12.3	12.3	12.3	12.3	12.3	12.3	12.3	12.3

Table XX. Oxygen levels with depth in spawning bed, Indian River Channel, 1966.

Date	Water Temp. °F	Above bed	Mean Sampling Depth Below Bed		
			5.5"	10"	16"
Oct. 25	38	11.8	11.5	11.8	3.2
26	41	11.8	11.5	11.4	3.3
	40	11.5	11.5	11.5	10.9
	39	11.8	11.8	11.6	10.9
	37	12.3	12.3	12.3	11.1

ruled out as an explanation because surface water temperature and water temperature measured at the 16" level were identical. Moreover, it is physically improbable due to the low perviousness of the substrate below the channel gravel.

The oxygen readings taken in the channel gravel indicate that percolation of water during spawning at the mean egg pit depth of 5.5 inches (Fig. 37) is probably quite adequate for egg incubation since readings only occasionally dropped below 10 ppm. However, oxygen of subsurface water at 5.5 inches never did reach full saturation but neither did water above surface. For both strata, saturation ranged from 91 per cent at the lowest water temperature recorded of 37°F to 84 per cent at the highest water temperature of 45.5°F. Oxygen dropped very significantly to 24 and 25 per cent saturation at 16 inches bed depth during the first two days of sampling this strata when water temperatures were 38°F and 41°F. This would indicate that due to the very poor permeability, water at 16 inches subsurface depth must be subject to fairly extensive stagnation. Whatever the cause of the partial saturations at surface and at egg depth, it is apparent that the effect is quite consistent with temperature, space and time (Fig. 37).

Although the oxygen sampling program did not, for the most part, support the findings of Chambers or Wickett within different spatial and vertical locations of the redd or within undisturbed spawning ground in the channel or in the river, it is apparent that gravel permeabilities in some of these studies were much lower than at Indian River. This is probably because channel gravel composition was screened of smaller fines while natural unscreened Indian River spawning gravel still remained very

porous compared to streams mentioned in the literature. Wickett (1954) at Nile Creek reports permeabilities which allowed his standpipes, after pumping off, to refill after 2 to 4 minutes. Such timed trials were never conducted in the channel or Indian River, but it is considered that channel or river standpipes following evacuation refilled much sooner than this, usually within a period of 30 to 60 seconds. After emptying a pipe, it was found that at the usual sampling depth of 5.5 inches, one could pump a further stroke of water from the pipe within a few seconds.

The use of dyes rather than oxygen as an indicator of subsurface current patterns through test plant mounds and redds was more informative. Placing the glass tube tip on the gravel bed surface resulted in the dyes disappearing into the upstream face of the mound but reappearing at the lower part of the downstream face of the mound within five to ten seconds time. Placing the tube tip at the base of the plant resulted in a dye cloud and circulation as shown in Fig. 38. A redd was examined in a similar fashion. Dye released upstream of the apical area at the gravel surface resulted in the same observation as at the plant mound (Fig. 39). The dye disappeared into the gravel and reappeared in five to ten seconds in the tail-spill region of the redd. This phenomenon was also witnessed intermittently if the tube tip was elevated about 1 to 1½ inches above the spawning gravel illustrating that a marked attraction into redd gravel exists adjacent the apex. However, if the tip was raised above about two inches, then a swift horizontal current over the redd carried the dye downstream past the apex. Placing the tip into the pot or excavation of the redd resulted in the cloud effect and an eddy as shown in Fig. 39. Burner (1951) and Hobbs (1948) observed a similar phenomenon in their examination of Pacific salmon and

brown trout redds in river spawning areas within the pots but did not note any downward attraction through the redd.

During 1966, only 5 of the 27 egg plants installed in spawning sections had redds attached to their upstream borders within a 1 to 9 day period following their burial (average time 4.5 days). This represents a substantial decrease in redd-test plant associations over 1965. This lower frequency of redd placement is mainly attributed to interferences caused by the oxygen sampling sequence. For five days after the test plants were installed (Fig. 37) the standpipes occupied the apical areas of the mounds and thereby obstructed spawning in the adjacent upstream bed. Walking daily onto these sites for oxygen determinations may also have caused some interference to spawning.

In retrospect, although subsurface oxygen was not a valid indicator of flow conditions in egg plant mounds or channel and river redds, the general hydraulic conditions of these structures in the stream bed were outlined using two different dyes. For the most part, Stuart's flume observations seem to apply in nature or at least in the channel environment. Hence, the writer feels justified in postulating that an area of subterranean current does exist in front of the egg plants which is preferred by Atlantic salmon spawners over other areas devoid of these or similar formations.

To a large extent, this explains why redds develop by the pattern they do. Females orient their digging and spawning according to the subsurface flow below the apex of a previous digging. They tend always to begin a further increment upstream to the mound whether this previous digging belongs to the female presently digging or whether it belongs to

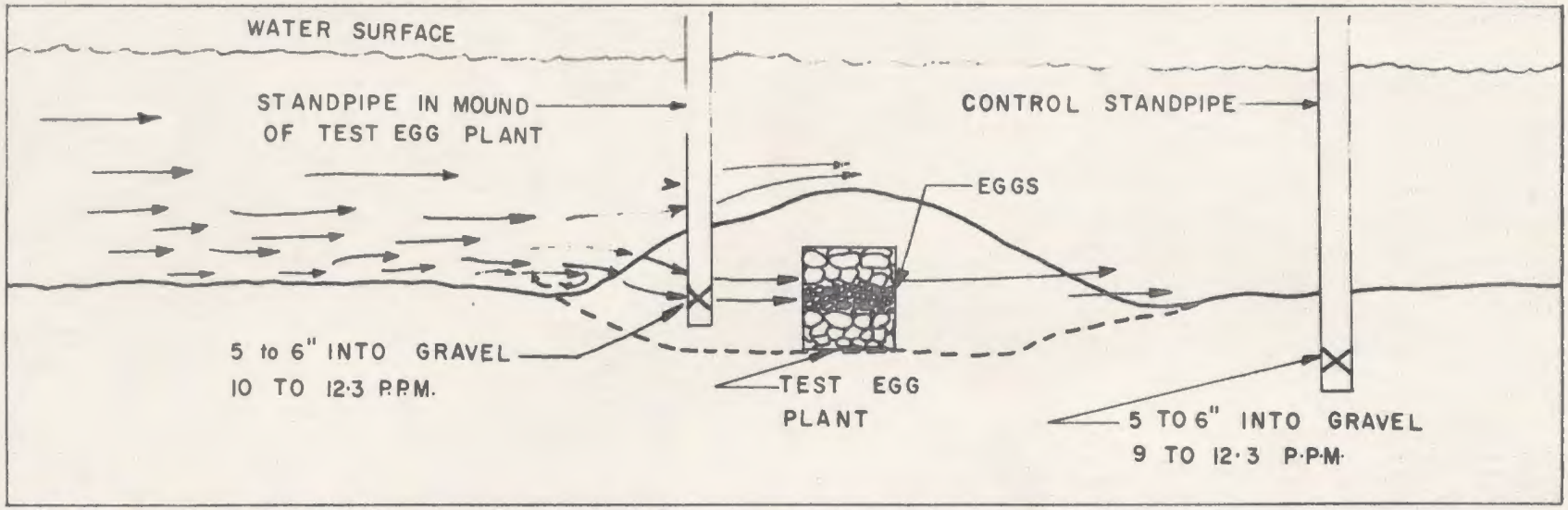
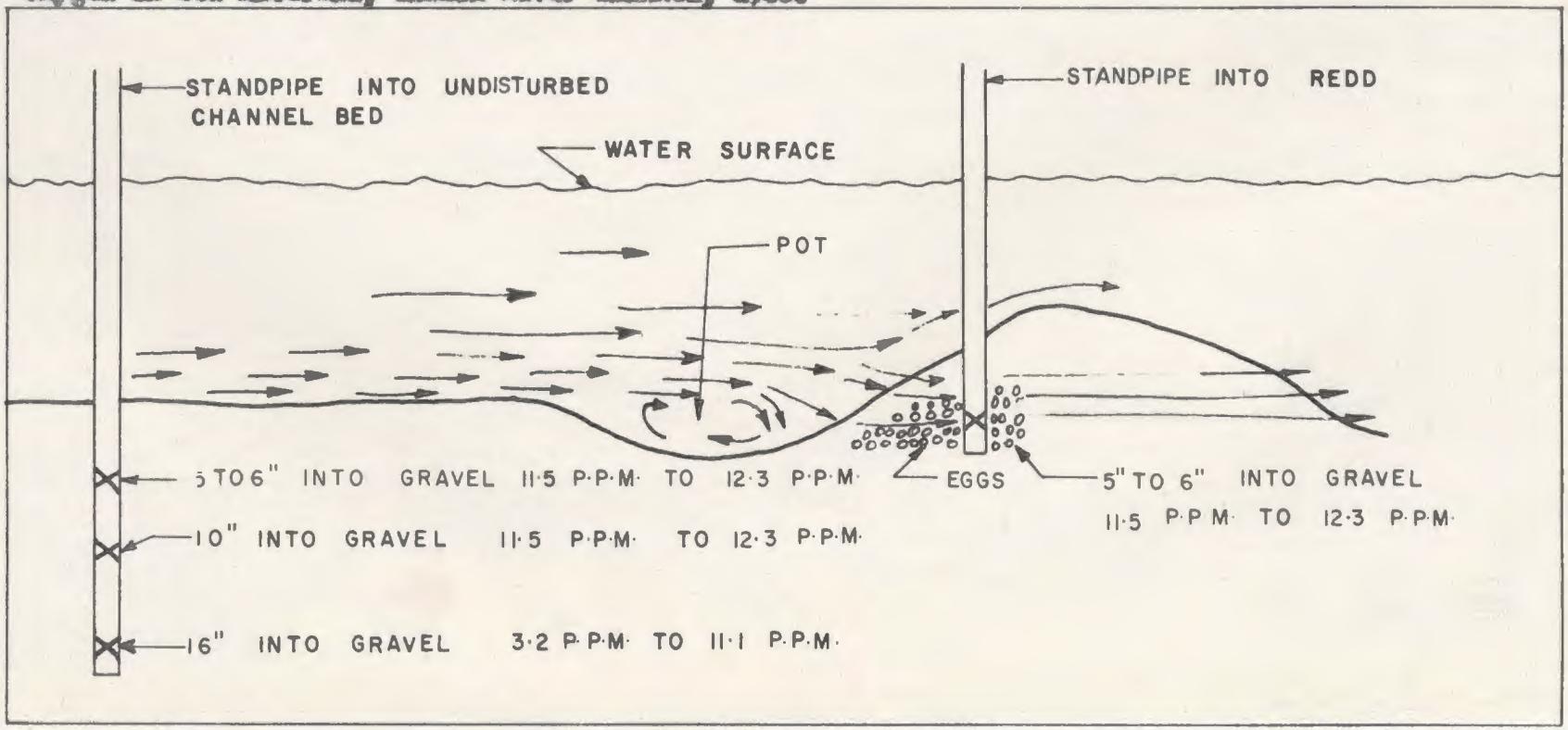


Fig. 38. Test egg plant buried in spawning bed with currents indicated along with positioning of standpipes, Indian River Channel, 1966.

Fig. 39. Redd with currents indicated along with positioning of standpipes used to study intragravel dissolved oxygen in bed material, Indian River Channel, 1966.



another female which abandoned it much earlier. The mound, because of its current qualities, acts as a stimulus to nest building.

If the relationship is as simple as this, it would also be reasonable to assume that salmon in an environment where bottom slope is constant, and gravel maintained permeable due to periodic screening and annual harrowing, would utilize any mound formation in the channel even those created in constructing trial or false redds. Such redds are frequently built in the channel up to 4 or 5 weeks before the beginning of actual spawning. They are small in area (usually less than 0.5 square yards), contain no eggs and are built only around the peripheries of holding pools. The distribution of 157 of these false redds placed in the channel by 80 females in 1963, was compared to the distribution of 85 true redds placed in the channel by this escapement in later weeks. However, mounds of only six of the trial redds were associated with six of the true redds. The trial redds were aggregated about holding pools while the true redds were distributed randomly over entire spawning areas. Because false redds have only minor mounds it may be that the hydraulic conditions necessary to attract spawning fish are not provided by these minor upheavals of the spawning bed.

4. Rock Weirs

It will be recalled that "staggered" and "V shape" rock weirs were erected in the channel in 1965. The only redd aggregation detected on the beds with Poisson and Negative Binomial analysis was on Spawning Area Four where one V-shape weir was located. According to the Poisson analysis, other spawning areas had random redd distributions indicating

that staggered weirs or other V-shaped weirs were not associated with any extensive redd clumping.

Dissolved oxygen readings are presented in Table XXI for three standpipes placed at the two cross sections adjacent the V-shaped weir. No notable differences are shown in dissolved oxygen from pipe to pipe within either cross section or between the cross sections, indicating the weir has not significantly modified the oxygen levels through width or length of this region of the channel. Since Coble's (1961) relationship between dissolved oxygen and apparent velocity in a streambed does not seem to apply, nothing can really be said regarding the subsurface current systems across or along the channel within this region of the bed.

Fig. 40 indicates the changes that occurred in water velocity and water depth at the three cross sections adjacent the weir. It can be seen that before the weir was installed, velocity and depth at particular points were fairly similar in all three cross sections. In the uppermost cross section, it is apparent that when the weir was built, velocity decreased, depth increased and channel width increased. At 0+72l, the presence of the weir's mouth did not alter velocity greatly but depth increased over the previous regime and channel width was curtailed due to the presence of the sides of the weir. At the lower cross section, an abnormal change in velocity occurred because of a severe flow constriction at the weir orifice but depth was quite similar to the profile which occurred before the weir was installed.

It appears then that water velocity and depth above the spawning bed have been altered by the presence of the weir. However, the area

Table XXI. Oxygen readings in two cross sections, one adjacent to and one upstream from weir, Indian River Channel, 1966.

Date	Pipes at weir p.p.m.			Pipes above weir p.p.m.		
	No. 1	No. 2	No. 3	No. 1	No. 2	No. 3
Oct. 20	11.8	11.5	11.5	11.8	11.5	11.5
Oct. 21	10.4	10.4	9.7	10.4	10.4	10.4
Oct. 22	11.4	11.4	11.4	11.4	10.8	11.4
Oct. 25	11.8	11.8	11.8	11.8	11.8	11.4
Oct. 26	11.4	11.8	11.4	11.4	11.8	11.4
Oct. 27	11.5	11.5	11.5	11.5	11.5	11.5
Oct. 28	11.6	11.6	11.6	11.6	11.6	11.6
Oct. 29	12.3	12.3	12.3	12.3	12.3	12.3

of the channel lying within the vicinity of these cross sections contained only one-third of the redds suspected of aggregating in 1965 with the largest clumping lying an additional 35 feet upstream from the uppermost cross section in Fig. 40 in a region where the effects of the weir's presence on water velocity and depth had almost disappeared. Five redds occupied most of the spawning area within the confines of the rock weir while three redds were placed in each of the two other V-type rock weirs erected on Spawning Area Six which also occupied much of ground within the weir. None of this crowding was extensive enough to be indicated as significantly clumped with the tests used in Tables IV and V.

White (1942) noted that Atlantic salmon in Nova Scotian streams dug their redds quite often at sites where current was accelerating and converging but just above the point of maximum convergence. Current

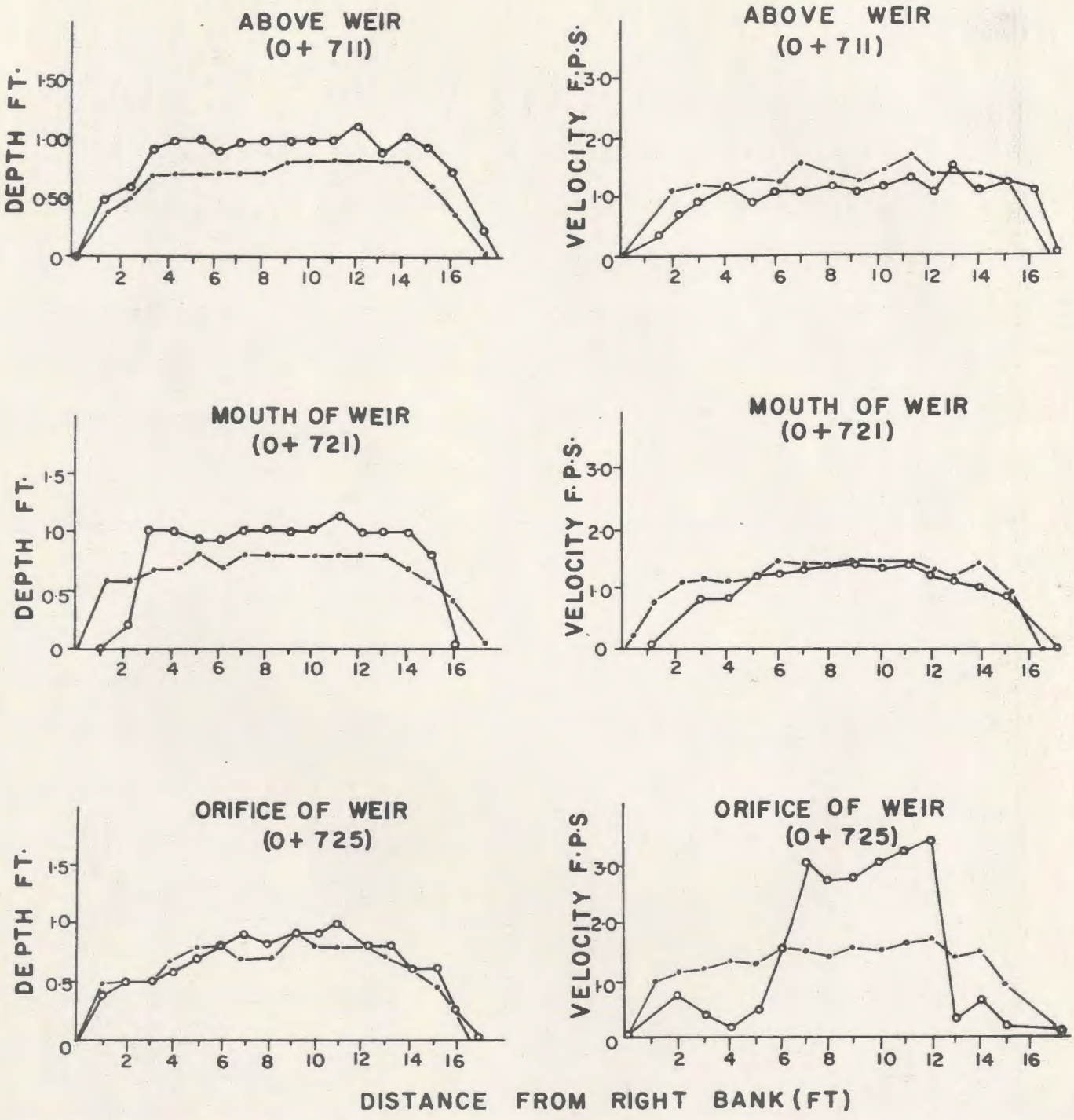


Fig. 40. Comparison of water depth and water velocity profiles before (---) and after (—o—) installation of V-shape rock weir, Spawning Area Four, Indian River Channel, 1966.

convergence was notable in all three rock weirs at Indian River Channel as was the gradient of current (Fig. 40). Furthermore, White also built several V-shaped bars out of stone very similar in configuration to the ones built in Indian River Channel with spawning beds built inside. The bars tended to create the current conditions mentioned above. Salmon were found to prefer these prepared sites for spawning over surrounding compacted areas. On the other hand, rock bars which he placed across brooks to raise the water level and cause part of the flow of the stream to pass over bars of loosened gravel resulted in salmon digging redds wherever the current conditions mentioned prevailed. This seems to indicate current convergence and gradient were the most important influences on redd digging in any of the created structures including the V-type rock weirs in the channel.

As for the major area of clumping 45 feet above the mouth of the weir on Area Four, it was wondered if this structure was not acting as a distributional barrier to fish between the two adjoining spawning areas. In 1965, it was noted that a proportionately larger number of fish resided in Pool Three than in Pool Four, the former being the deepest of the two. Also, Table VIII and Fig. 24 show that Spawning Areas Three and Four bordering Pool Three were highly utilized with significant clumping on part of Area Four upstream of the weir. On the other hand, the spawning area surrounding Pool Four (i.e. Area Five and the lower part of Area Four below the weir) was lightly utilized. Adults moving out from the adjoining pools may be somewhat deterred from moving freely upstream or downstream past the weir because of the abrupt velocity gradient at the orifice (Fig. 40). More important, the weir may provide a

bottleneck to distribution because of territorial behavior at this point. Pairs of fish spawning in the confines of the weir especially in the area of maximum current convergence just a few feet above the orifice would most certainly defend much of this narrow passageway as breeding territory and tend to attack all foreign spawners moving through the orifice. Datings of redd increments just upstream of the orifice, and at the point of major clumping indicate that most of the spawning in these regions occurred within the same ten day period. Thus, territorial defense must have predominated at the weir during peak spawning and possibly served to concentrate spawning above the weir.

Aggregation was not detected in 1966 on Spawning Area Four about the weir according to Table IV but three redds were still present utilizing about one half of the spawning area within the weir. Nonetheless, although Column 6 of the table indicates that Section IV was acceptably random, Column 7 shows that the frequency of redds provided by the Section with Area Four deleted approximates the Poisson Distribution more so. Less spawning and agonistic activity over the weir spawning bed, more even densities of fish in Pools Three and Four, added human interference about the weir in taking oxygen readings are all factors which may have acted or interacted to result in this more random distribution.

5. Pool and Spawning Bed Shelters

Most of the spawners residing in the holding pool with the plywood shelter congregated directly beneath it. Figure 41 illustrates the distribution of spawners in the pool. Most of the fish stayed under the shelters whether day or night, but higher percentages remained exposed

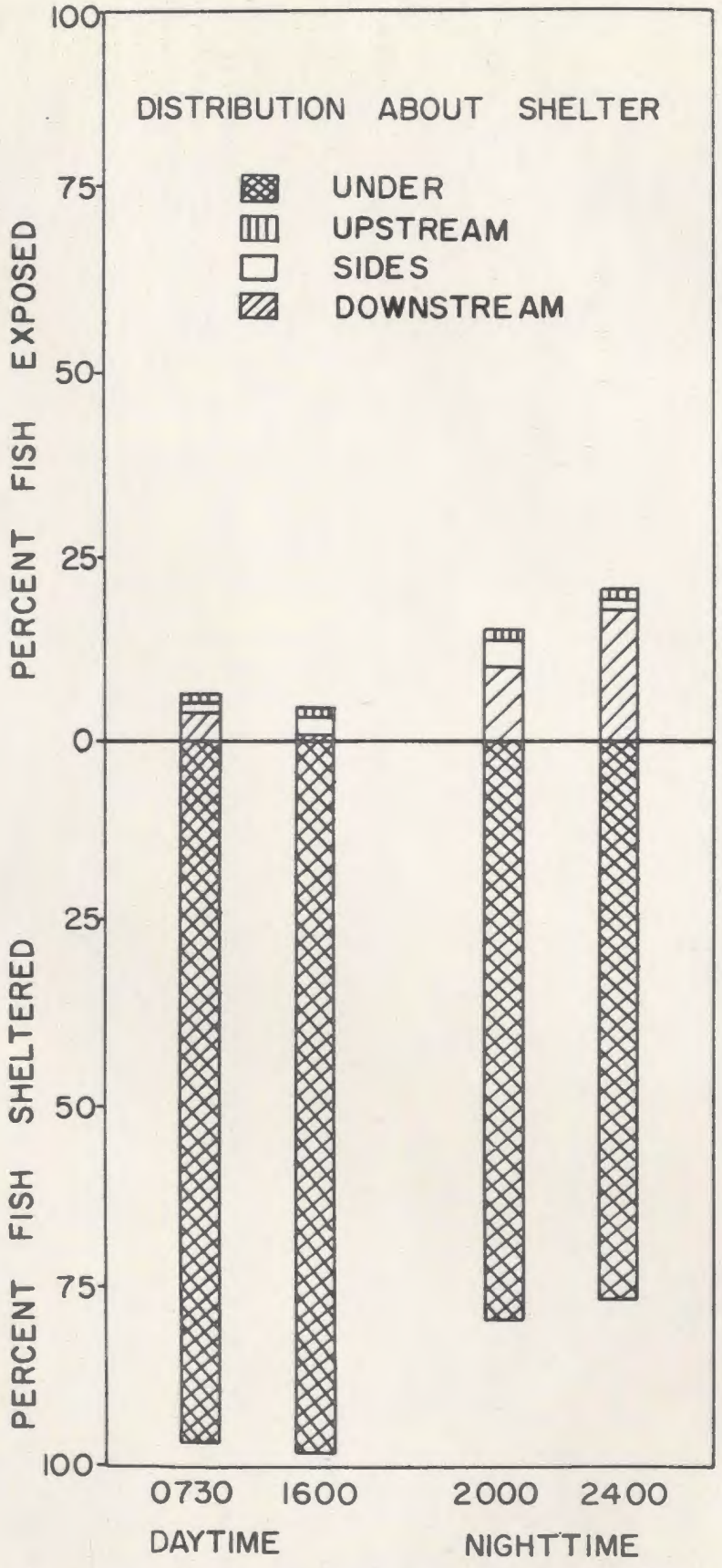


Fig. 41. Distribution of spawners about shelter placed over Pool One, Indian River Channel, 1966.

in the pool during the nighttime. Over the spawning period, fish exposed distributed themselves mainly downstream of the shelter with very few being recorded upstream or to the sides of the shelter.

It may be that light intensity is an influence on whether spawners seek shelter in holding pools. More fish were exposed at night and fewer during the day, but to accurately assess this phenomenon, a sensitive underwater photometer would be needed to take daily light readings both under and about the shelter.

It appears that spawners on the beds are not attracted to floating shelter. Of sixty-five checks made on the spawning bed shelter, one fish was found under the shelter only during two successive evening checks, at the very end of the spawning season. No redd activity was located beneath or adjacent the shelter.

C. Management Implications

1. Channel environment

One of the problems in operating controlled flow channels for Atlantic salmon spawners is to determine the highest density of spawners which can safely be used, bearing in mind the limitations of spawning distribution and channel design. At the outset, one realizes there is no one figure or range of figures that can be devised for universal application to Atlantic salmon channels since variability in characteristics of spawning populations and changes in design of facilities will probably prevail.

At Indian River, according to the statistical measurements employed, the spawning distributions were largely random although clumping

about weirs was observed along with some spatial changes in bed utilization. At the highest density of one female per six or seven square yards, thirteen per cent of the total redd area was superimposed, and this was probably responsible for a lower than anticipated egg-to-fry survival from the spawning bed. Moreover, the redd space to inter-redd space ratio is similar to maximum spawning densities quoted for other salmonids (Burner, 1951; Stuart, 1960). Hence, this capacity figure for the channel should be viewed as an allotment approaching the practical management threshold. This means that no more than 300 to 350 fish should ever comprise the escapement to Indian River Channel with the size composition, sex ratio and physical conditions which exist.

However, the possibility still exists that although some critical redd overlap did occur, it may not become that significant until a much higher spawning density is reached especially if the area of digging per female continues to decrease. Moreover, Sections II and III held at the highest spawning density (Fig. 25) still had several quadrats with no redds plotted. For this reason, it is recommended that the above allotment be used as a maximum until further experiments can be carried out at still higher spawning densities to finalize if the present figure is the most practical and beneficial to management.

As mentioned earlier, the channel management of the Indian River escapement will probably not apply precisely to salmon in channels on other rivers since the populations in them will likely be somewhat different in biological characteristics. However, the writer considers it safe to make some general statements about management of Atlantic

salmon runs of the three to five pound weight class especially since preliminary results gathered on a second grilse population at Noel Paul's Channel with slightly different body size and quite different sex ratio were consistent with Indian River results.

The gradient and hydraulic design at Indian River Channel appeared satisfactory for adult distribution. There would seem to be little advantage to altering the water velocity and depth regimes now used with grilse runs.

Still holding pools four or five feet in depth spaced at intervals throughout the beds are considered important to the survival and distribution of the adults while they reside in the channel. Newfoundland grilse mainly enter rivers in June, July and August to spawn in October and November. This means part of the spawning runs may enter a channel and remain there in a pre-spawning state for more than three months. Absence of resting pools over this period of time would obviously expose the escapement to additional stresses of water current and predation. Furthermore, staggering suitable pools throughout the channel's length probably ensures more even utilization of the spawning area since the presence of one shallow sparsely populated pool at Indian River was associated with lower utilization of the adjacent spawning bed.

Shelter also seemed to affect adult distribution within pools and may govern distribution to pools to some extent. On the other hand, shelter over spawning beds did not seem to affect spawning distribution.

Other man-made structures on spawning beds such as rock weirs

were of little advantage in operating a channel and may have served in certain cases as a barrier to spawning distribution.

The composition of spawning gravel seemed quite suitable to spawning distribution as would be expected, considering it was screened to range within the limits which Atlantic salmon are known to utilize in nature anyway. The spawning material should be spread in a deep layer on the channel bottom because small three pound grilse placed their eggs in pits dug as deeply as ten inches. Many Newfoundland grilse spawners may average somewhat larger in size. Placing gravel in a layer averaging 24 inches on the channel bottom should allow for any anticipated increase in bed penetration and allow satisfactory bed seepage provided a continuous schedule for cleaning gravel is maintained. In this regard, annual hand spading of bed rather than harrowing is recommended since the latter method tended to change channel water profiles and possibly the spawning utilization of sections of width within the bed. Spawning gravel may also have to be removed, screened and washed of silt periodically dependent on how effective the annual spading method proves as shown by annual gravel grading analysis and by annual egg-to-fry survival rates.

Work with test egg plants suggests that channel spawning distribution might be effectively controlled by the biologist. Further investigations utilizing mounds and other prepared formations might result in development of a way to evenly distribute spawning reducing the egg mortality caused from overspawning.

In a situation where bottom type is small, bank and channel gradients are constant, the visual isolation provided between pairs is

low. Channel widths of sixteen feet with the present bottom profiles hardly allow two pairs room to spawn beside each other without significant overlaps and interferences between spawning territories. Without greatly altering the water depth and velocity profiles, there might be merit in conducting experiments with increased channel widths or with standard widths but partitions installed which are penetrable to fish. Such partial barriers might be realized by placing gravel, rocks or boulders into low subsurface berms in some configuration which would reduce visibility between pairs spawning alongside but would still allow free passage of fish over the spawning areas.

Regarding utilization of channels by other fish besides adult Atlantic salmon, it is deemed advisable to exclude salmon parr and other species so as to avoid further egg predation observed in parr and trout populations. Any advantage afforded salmon egg fertilization by residing male parr is probably more than balanced by the eggs they eat.

2. River Environment

For many years, the Resource Development Branch of the Department of Fisheries in Newfoundland has been conducting spawning surveys on streams after the spawning season has finished in an attempt to establish the magnitude of the spawning escapements. These surveys generally consist of walking or floating streams and noting the number and location of the redds. This type of survey usually pinpoints the main spawning areas and gives one some idea of annual fluctuations in runs, but it tells one little about the actual size of the escapement, because it is unknown how many redds can be attributed to each pair, female or

fish. With Atlantic salmon spawners, it is not possible to do a fish count on the spawning beds since they tend to be very elusive creatures. Moreover, it is generally not possible to conduct reliable counts or estimates during their early migration into the river since counting weirs are not usually available.

At Indian River Channel, from daily plotting of increments into the redds, it has been possible to consistently separate these workings as definite spatial entities. However, on the natural spawning grounds of a river, it is very difficult to define redds this exactly. In fact, it is often impossible to even recognize the exact peripheries of them, two or three weeks after they are built. Hence, an area of digging which might be deciphered by daily plotting as two or three distinct redds by the criteria employed at the channels, merely appears with one visit at the end of the season as one large mass of undifferentiated digging which one is forced to call one redd.

To cast some light onto the significance of this discrepancy, channel redds which were plotted and counted on the exact basis, were recounted ignoring all the temporal information concerning the increments. This meant that where spatial overlaps between two known redds existed, they were often recounted as one redd. Both counts were then related to the known annual escapements of the channel.

It can be seen from Table XXII that with the precise count in 1965 and 1966 at the channel, there was roughly one redd plotted for every fish in the escapement or about 1½ redds for each female occupant. On the other hand, a recount in these years after redd activity was finished neglecting the dating of increments indicates much less than

Table XXII. True and apparent redd counts related to annual spawning escapements, Indian River Channel, 1963 - 1966.

Year	Exact count of redds		Apparent count of redds	
	Redds per fish	Redds per female	Redds per fish	Redds per female
1963			0.76	1.06
1964			0.75	1.00
1965	0.97	1.26	0.72	0.94
1966	0.98	1.25	0.68	0.87
Average	0.98	1.26	0.73	0.97

one redd per fish in the channel and approximately one redd per female. In 1963 and 1964, redd counts were conducted only in this way and are included in the table. It is evident that the redds per fish or per female figures compare closely to the superficial channel recounts of 1965 and 1966.

In summary, with continuous temporal plotting, it appears that there is roughly one redd per fish counted in the channel while with single post spawning surveys only one redd per female is counted. It is believed that this information may prove useful in estimating natural spawning populations on Indian River and other streams if further testing indicates that these relationships apply to natural spawning conditions. The formula:

$$\text{Size of spawning population} = \frac{\text{number of apparent redds counted}}{\text{proportion of females in population}}$$

which applies to Indian River Channel will be applied to Indian River itself and checked for validity in oncoming years. This will be done by

continuing the redd surveys and comparing the annual estimated size of the population from the above formula to actual adult counts now possible on this river because of a newly erected counting fence on the lower portion of the watershed (Fig. 1).

How reliable this formula may prove, remains to be seen. Even if it produces accurate estimates at Indian River, it would be advisable to further test the relationship by selecting an additional stream whose grilse population is quite different in size and sex composition. If the ratio of one redd per female is still upheld, then there should be reason to be optimistic that the relationship is applicable to other rivers.

IV. SUMMARY and CONCLUSIONS

1. Atlantic salmon were observed to spawn in controlled flow channels located at Indian River and Noel Paul's Brook very successfully free of disease or serious egg retention. Condition of spawners remained excellent throughout the season with mortality from predation serious in only one year at Indian River when it was necessary to exercise control measures with a local mink population.

2. Spawning of adult Atlantic salmon was observed both within the Indian River Spawning Channel and within a specially built observation chamber. The general sequence of spawning was established starting with the digging action by the female, including one orgasm between the pair and ending with covering of the fertilized eggs in gravel by the female.

3. Both members of the spawning pair displayed agonistic reactions towards intruders in defending their breeding territories which centered about the redds or egg nests. In most cases, the territory was quite transitory both in regard to spawning location and spawning mate. Females did not always place all their spawnings into one redd and it was common to observe more than one female contribute to the spatial entity of the redd.

4. The redd distributions in Indian River Channel mainly conformed to a hypothesis of random distribution at the spawning densities examined. Contagious and dispersive elements were noted along with spatial changes in the utilization from spawning bed to spawning bed and from center to edge of the channel. Contagion or clumping

of redds was observed with the scales of measurement employed only in one year on one spawning bed containing a V-shaped rock weir. The changes in utilization of spawning areas were largely attributed to changes in the density of spawners residing in the holding pools. The increased use of channel shoreline during the last year of study was attributed to physical alterations of the water depth profiles adjacent the edges which allowed spawners to locate more of their redds along the banks than in previous years.

5. As the densities of spawners at Indian River Channel increased, the redd area utilized by each female diminished but redd superimposition still continued to increase. At the highest spawning density imposed which was one female per 6.4 square yards, roughly one quarter of the channel spawning bed was placed into redds with 13 per cent of the redd area superimposed. The available evidence suggests that this density of spawners may be approaching a practical capacity but higher densities should be tested before adopting this space allotment in managing the channel.

6. Daily fluctuations in water temperature and light intensity at Indian River appear connected with daily changes in the numbers of fish moving from holding pools to spawning areas. The degree of relationship between water temperature and spawning activity was observed to be significant in the first year of study but insignificant the next - a phenomenon which could not be explained. A statistical analysis of light was not possible due to lack of instrumentation.

7. Adults, when choosing sites for spawning, appear quite flexible in their choice of water velocity and water depth which is largely a reflection of the water velocity and depth available. The spawning distributions indicate that any particular subrange of depth or velocity lying within the narrow regime provided by channel design is as suitable as any other to management.

8. From subsurface current studies within mounds created in burying test egg plants, it is postulated that an area of maximum subterranean current exists on the forward slope of such mounds. This area of vertical circulation into the mound attracts adults over other areas devoid of these or similar formations. It is believed that this partly explains why redds develop by the pattern they do with females orienting their digging and spawning according to the subsurface flow upstream of the apex of the previous digging. The effect of the test plant mounds was sufficiently marked to suggest that spawning distribution might be effectively controlled within channels by utilizing such mound formations.

9. The presence of a V-shaped rock weir on one spawning bed was coincident with significant clumping of the redd distribution. The structure appeared to act as a distributional barrier probably because of territorial behaviour released by pairs spawning within the confines of the weir and possibly because of a sharp current gradient existing at the downstream orifice. Hence, weirs of staggered or V-shape variety appear to be of no management advantage in channels.

10. Most spawners residing within one channel holding pool were observed to congregate beneath a plywood shelter placed in it. Spawners showed no preference for spawning area covered by a second shelter.

11. Eventually, a method of estimating stream spawning escapements by counting the redds on spawning grounds may be possible in certain situations but further testing of the method is still necessary.

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VI. REFERENCES

ANDREWARTHA, H.G. 1963. Introduction to the study of animal populations. Phoenix Science Series, Univ. Chicago Press.

BLISS, C.J. 1953. Fitting the negative binomial distribution to biological data and a note on the efficient fitting of the negative binomial. Biometrics, 9: 176-200.

BRIGGS, J.C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. Calif. Dept. Fish. and Game. Mar. Fish. Br. 94 (1): 1-62.

BURNER, C.J. 1951. Characteristics of spawning nests of Columbia River salmon. U.S. Fish. Wildl. Serv. 52 (61): 97-110.

CHAMBERS, J.S., G.H. ALLEN and R.T. PRESSEY. 1955. Research relating to study of spawning grounds in natural areas. Ann. Rep. Wash. Dept. Fish. to U.S. Army Corps. Eng.

COBLE, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Trans. Amer. Fish. Soc. 90 (4): 469-474.

CROXTON, F.E. and D.J. COWDEN. 1956. Applied general statistics. 2nd ed. Prentice-Hall Inc., Englewood Cliffs, N.J.

DAVIDSON, J. and H.G. ANDREWARTHA. 1948. The influence of rainfall, evaporation and atmospheric temperature on fluctuations in size of a natural population of Thrips imaginis (Thysanoptera). Jour. Anim. Ecol. 17: 200-222.

FABRICIUS, E. 1952. Aquarium observations on spawning behavior of S. alpinus. Rept. Inst. Freshwater Res. Drottningholm. 34: 14-48.

FABRICIUS, E. and K. GUSTAFSON. 1953. Further aquarium observations on the spawning behavior of char. Rept. Inst. Freshwater Res. Drottningholm. 35: 59-101.

FABRICIUS, E. and K. GUSTAFSON. 1954. Observations on the spawning behaviour of the grayling. Thymallus thymallus (L.) Rept. Inst. Freshwater Res. Drottningholm. 29: 35-44.

GANGMARK and BAKKALA. 1958. A plastic standpipe for sampling the streambed environments of salmon spawn. U.S. Fish and Wildl. Serv. Spec. Sci. Rept. Fish. 261: 1-20.

GRANT, A.A. 1963. Studies of regeneration in forest stands devastated by the spruce budworm. III. Problems of sampling precision and seedling distribution. Forest Science 9 (3): 295-310.

GILBERT, C.H. and W.H. RICH. 1927. Investigations concerning the red salmon runs to the Karluk River, Alaska Bull. U.S. Bur. Fish. 43(2): 1-69.

GRANLEY, J.L. 1932. The spawning habits of brook, brown and rainbow trout, and the problem of egg predators. Trans. Amer. Fish. Soc. 62: 239-248.

GUSTAFSON, K.J. 1948. Movements and growth of grayling. Rept. Inst. Freshwater Res. Drottningholm. 29: 35-44.

HAZZARD, A.S. 1932. Some phases of the life history of the eastern brook trout. Trans. Amer. Fish. Soc. 62: 344-350.

HOBBS, D.F. 1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters, N.Z. Mar. Dept. Fish. Bull. 6: 1-104.

HOBBS. D.F. 1940. Natural reproduction of trout in New Zealand and its relation to density of populations. N.Z. Mar. Dept. Fish. Bull. 8: 1 - 93.

HOBBS, D.F. 1948. Trout fisheries in New Zealand, their development and management. N.Z. Mar. Dept. Fish. Bull. 9: 1-175.

HOUSTON, W.R. and D. MACKINNON. 1956. Use of an artificial spawning channel by salmon. Trans. Amer. Fish. Soc. 86: 220-230.

JONES, J.W. and C.M. King. 1949. Experimental observations on the spawning behaviour of the Atlantic salmon (Salmo salar). Zool. Soc. Lond. Proc. 119: 33-48.

JONES, J.W. and C.M. KING. 1950. Further experimental observations on the spawning behaviour of the Atlantic salmon (Salmo salar). Zool. Soc. Lond. Proc. 120: 317-323.

JONES, J.W. and J.N. HALL. 1953. The spawning behaviour of brown trout and salmon. Brit. Jour. Anim. Behav. 1:103-114.

JONES, J.W. 1959. The salmon. Collins, St. James Place, London.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). Rept. Inst. Freshwater Res. Drottningholm, 39: 55-98.

LINDROTH, A. 1954. A stream tank of the Holle laboratory. Rept. Inst. Freshwater Res. Drottningholm, 35: 113-117.

MACKINNON, D., L. EDGERTH and R.B. MCLAREN. 1961. An assessment of Jones Creek Spawning Channel. 1954-1961. Can. Fish. Cult. 30: 3-14.

MATHISEN, O.A. 1962. The effect of altered sex ratios on the spawning of red salmon. Univ. Wash. Pub. Fish. 1: 139-245.

McNEIL, W.J. 1962. Variations in the dissolved oxygen content of intragravel water in four spawning streams of southeastern Alaska. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 402: 1-15.

McNEIL, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. J. Fish. Res. Bd. Canada, 21(6): 1385-1396.

McNEIL, W.J. 1966. Distribution of spawning pink salmon in Sashin Creek, Southeastern Alaska and survival of their progeny. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 538: 1-11.

McNEIL, W.J. 1967. Randomness in distribution of pink salmon redds. J. Fish. Res. Bd. Canada. 24(7): 1629-1634.

NEEDHAM and TAFT. 1934. Observations on the spawning of steelhead trout. Trans. Amer. Fish. Soc. 64: 332-338.

NOBLE, G.K. 1939. The role of dominance in the social life of birds. Auk. 56: 263-273.

PRATT, J.D. 1964. A controlled flow spawning channel for Atlantic salmon, Indian River, Newfoundland. Proj. Rept. Fish. Cult. Dev. Br., Dept. Fish. Canada, St. John's.

PRATT, J.D. and C.C. STURGE. 1965. Indian River Studies, 1964-1965, Proj. Rept. Fish. Cult. Dev. Br., Dept. Fish. Canada, St. John's.

REINHOLD, M. 1965. in Orcutt, D.R., B.R. Pulliam and A. Arp, 1968. Characteristics of steelhead trout redds in Idaho streams. Trans. Amer. Fish. Soc. 97(1): 42-45.

STUART, T.A. 1953. Water currents through permeable gravels and their significance to spawning salmonids, etc. Nature, London. 172: 407-408.

STUART, T.A. 1954. Spawning sites of trout. Nature, London. 173: 354.

TERHUNE, L.D.B. 1958. The Mark VI groundwater standpipe for measuring seepage through salmon spawning gravel. J. Fish. Res. Bd. Canada. 15 (5): 1027-1063.

TINBERGEN, N. 1953. Social behaviour in animals. Methuen and Co. Ltd., London.

WHITE, H.C. 1930. Some observations on S. fontinalis of P.E.I. Trans. Amer. Fish. Soc. 60: 101-108.

WHITE, H.C. 1942. Atlantic salmon redds and artificial spawning beds. J. Fish. Res. Bd. Canada. 6 (1): 37-44.

WICKETT, W.P. 1954. The oxygen supply to salmon eggs in spawning beds. J. Fish. Res. Bd. Canada. 11 (6): 933-953.

VII. APPENDIX - Tables

Table I . Basic data used in comparing redd distributions to Theoretical Poisson Distribution, Indian River Channel, 1965, 1966.

	1965													1966				
	Section		Section III excl. Area No.					Spawning Area No.						Section			Section IV excl. Area No. 4	Sp. Ar. No. 4
	II	III	2	3	4	5	6	1	2	3	4	5	6	II	III	IV		
N	21	186	144	146	144	146	164	42	42	40	42	40	22	14	42	144	102	42
$\sqrt{\bar{x}}$	0.707	0.789	0.768	0.735	0.781	0.848	0.807	0.707	0.859	0.961	0.816	0.524	0.639	1.22	1.06	0.707	0.714	0.69
$\sigma = \sqrt{\frac{\Sigma x^2 fo - \bar{x}(\Sigma xfo)}{N-1}}$ [1]	0.594	0.887	0.864	0.871	0.845	0.937	0.903	0.594	0.964	0.868	1.028	0.553	0.734	1.34	1.05	0.728	0.749	0.63
$diff = \sigma - \sqrt{\bar{x}}$	-0.113	0.098	0.096	0.136	0.064	0.089	0.096	-0.113	0.105	-0.093	0.204	0.029	0.095	0.12	-0.01	0.021	0.035	-0.06
S.E. $diff.^2 = \sqrt{\frac{\bar{x}}{2N}}$	0.077	0.041	0.045	0.042	0.046	0.049	0.042	0.077	0.094	-0.107	0.089	0.058	0.096	0.238	0.114	0.041	0.050	0.08
$t = \frac{diff.}{S.E.\ diff.}$	-1.467	2.39	2.13	3.23	1.39	1.80	2.28	-1.47	1.12	-0.867	2.29	0.50	0.99	0.43	0.08	1.95	0.700	-0.80
$> P >$	.2-.1	.05-.02	.05-.02	.005-	.2-.1	.1-.05	.05-.02	.2-.1	.3-.2	.4-.3	.05-.02	.7-.6	.4-.3	.7-.6	1.0-.9	.1-.05	.5-.4	.4-.3

[1] σ = Standard Deviation

[2] S.E. = Standard Error

Table II(a). Basic data used in comparing redd distributions to Negative Binomial Distribution, Indian River Channel, 1965 (after Elliot, 1953).

No. redds per quadrat (x)	Section III excl. Area No. 4				Section III incl. Area No. 4				Area No. 4			
	No. of quadrats obs. (f)	Accum. frequencies (Ax)	Expected frequencies ϕ	$\frac{(f-\phi)^2}{\phi}$	f	Ax	ϕ	$\frac{(f-\phi)^2}{\phi}$	f	Ax	ϕ	$\frac{(f-\phi)^2}{\phi}$
0	83	61	81.88	0.02	109	77	106.90	0.04	26	16	26.00	0.00
1	41	20	42.78	0.07	49	28	52.81	0.28	8	6	9.26	0.17
2	13	7	14.27	0.11	18	10	18.53	0.02	5	3	3.80	0.37
3	7	0	3.86	2.54	9	1	5.62	2.03	2	1	1.63	0.08
4	0	0	1.18	1.18	1	1	2.12	0.99	1	1	1.29	0.07
5	0	0	0.00	0.00	0	0	0.00	0.00	0	0	0.00	0.00
Total	144=N		143.97	3.92(χ^2)	186=N		185.98	2.96(χ^2)	42=N		41.98	0.69

Table II(b). Basic data used in comparing redd distributions to Negative Binomial Distribution, Indian River Channel, 1965 (after Elliot, 1953).

Statistic	Section III excl. Area No. 4	Section III incl. Area No. 4	Area No. 4
S(fx)	88.00	116.00	28.00
$S(fx^2)$	156.00	218.00	62.00
$\bar{x}$	0.61	0.62	0.67
s^2	0.72	0.79	1.06
$\hat{k}$ (most probable)	method 1: 3.60	method 1: 2.38	method 2: 0.77
$V_{\bar{x}}$	0.01	0.00	0.03
$s_{\bar{x}}$	0.07	0.07	0.17
$V_{\hat{k}}$	10.93	2.00	0.24
$s_{\hat{k}}$	3.31	1.41	0.49

Table III Basic data used in comparing observed and expected redd numbers in given width intervals, Indian River Channel, 1963-1966.

Year	Section	Right Periphery		Centre		Left Periphery		Chi square	>P>
		Observed freq.	Expected freq.	Observed freq.	Expected freq.	Observed freq.	Expected freq.		
1963	full channel	24	28.3	23	28.3	38	28.3	4.96	.1 - .05
1964	full channel	74	67.6	61	67.6	68	67.6	1.26	.7 - .5
1965	II	8	7	6	7	7	7	0.28	.7 - .5
	III	42	38.7	45	38.7	29	38.7	3.73	.2 - .1
	III excl. No. 4	33	29.3	35	29.3	20	29.3	4.47	.2 - .1
1966	II and III	34	23	13	23	22	23	9.64	.05 - .025
	IV	31	24	13	24	28	24	6.07	.05 - .025
	IV excl. No. 4	22	17.3	9	17.3	21	17.3	6.02	.05 - .025

Table IV. Basic data used in comparing observed and expected redd numbers on sections with free dispersal over two or more spawning areas, Indian River Channel, 1965, 1966.

Spawning Area No.	Length (Ft.)	Area yd.^{2}	1965		1966	
			No. redds observed	No. redds expected	No. redds observed	No. redds expected
2	168	298.6	31	26.19		
3	160	284.4	37	24.95	22	20.00
4	168	298.6	28	26.19	20	21.00
5	160	284.4	11	24.95	16	20.00
6	88	156.4	9	13.72	14	11.00
Chi square			16.35		1.87	
>P>			.005 - .001		.7 - .5	

Table V. Basic data used in calculating significant differences between means for depth and velocity preference during spawning, in various sections, Indian River Channel, 1965, 1966.

Year	Section	N	Velocity					Depth				
			Range	Mean	S.D.[1]	t value	>P>	Range	Mean	S.D.	t value	>P>
1965	II	20	0.9 - 2.1	1.495	0.338			0.5 - 1.4	0.745	0.214		
						0.9	.4 - .3				0.6	.6 - .5
	III	114	0.4 - 2.7	1.263	0.378			0.5 - 2.1	0.841	0.246		
	II and III	134	0.5 - 2.7	1.305	0.383			0.5 - 2.1	0.827	0.244		
1966	II	18	0.3 - 1.2	0.80	0.358			0.5 - 2.3	1.45	0.340		
						2.1	.05 - .02				2.7	.01
	III	48	0.5 - 2.0	1.12	0.285			0.7 - 2.3	1.21	0.298		
	II and III	66	0.3 - 2.0	0.99	0.285			0.5 - 2.1	1.27	0.284		
						4.0					4.6	
	IV	71	0.5 - 2.0	1.16	0.258			0.7 - 1.7	1.10	0.182		

[1] S.D. = Standard Deviation

Table VI Basic data used in calculating significant differences between mean depth and velocity redd preferences by section of width and spawning section, Indian River Channel, 1965, 1966.

Year	Spawning Section	Velocity, f.p.s.					Depth, ft.		
		Width Section[1]	N	Mean	S.D.[2]	2 S.E.[3]	Mean	S.D.	2 S.E.
1965	III	right	43	1.24	0.417	0.127	0.72	0.168	0.051
		centre	43	1.38	0.373	0.114	0.84	0.222	0.067
		left	28	1.18	0.325	0.123	0.89	0.308	0.116
1966	II and III	right	32	0.92	0.222	0.077	1.15	0.390	0.137
		centre	12	1.19	0.325	0.188	1.30	0.188	0.109
		left	21	0.96	0.339	0.148	1.32	0.272	0.118
-	IV	right	30	1.09	0.198	0.072	1.01	0.175	0.064
		centre	13	1.27	0.240	0.133	1.16	0.225	0.125
		left	28	1.19	0.297	0.112	1.07	0.157	0.059

[1] looking downstream

[2] SD = Standard deviation

[3] SE = Standard error

Table VII. Polynomial Curves fitted to trends of observed values for water temperature (°F) and spawning activity (no. of fish), Indian River Channel, 1965, 1966.

Year	Description of data	Equation for line of best fit	N	$\sqrt{\Sigma(Y - Yc)^2}$
1965	Temperature trend daybreak period	$Yc = 44.079 - .216X - .013X^2 + .0003X^3$	28	13.209
	Temperature trend afternoon period	$Yc = 47.995 - .563X + .008X^2 - .0003X^3$	28	10.879
	Temperature trend evening period	$Yc = 47.034 - .340X - .005X^2 - .0006X^3$	28	11.323
	Temperature trend midnight period	$Yc = 44.784 + .114X - .036X^2 + .0005X^3$	28	12.099
	Activity trend daybreak period	$Yc = 22.133 - 6.076X + .559X^2 - .014X^3$	13	16.848
	Activity trend afternoon period	$Yc = 205.901 - 46.703X + 3.397X^2 - .073X^3$	10	31.911
	Activity trend evening period	$Yc = 548.072 - 95.093X + 5.503X^2 - .105X^3$	15	27.116
	Activity trend midnight period	$Yc = 26.702 + 1.200X - .042X^2 + .0005X^3$	16	10.731
1966	Temperature trend daybreak period	$Yc = 46.770 + .444X - .049X^2 + .0006X^3$	29	17.693
	Temperature trend afternoon period	$Yc = 66.709 - 1.682X + .029X^2 - .0009X^3$	28	17.083
	Temperature trend evening period	$Yc = 74.296 - 2.316X + .047X^2 - .0003X^3$	28	31.641
	Temperature trend midnight period	$Yc = 69.255 - 1.838X + .029X^2 - .0003X^3$	29	15.805
	Activity trend daybreak low density	$Yc = -28.190 + 1.655X - .009X^2 - .0004X^3$	20	9.625
	Activity trend afternoon low density	$Yc = 333.499 - 38.993X + 1.491X^2 - .018X^3$	17	19.412
	Activity trend evening low density	$Yc = 219.277 - 21.056X + .761X^2 - .008X^3$	18	31.641
	Activity trend midnight low density	$Yc = -70.120 + 3.848X + .092X^2 - .004X^3$	20	22.943
	Activity trend daybreak high density	$Yc = -2.771 - .407X + .041X^2 - .0007X^3$	21	6.095
	Activity trend afternoon high density	$Yc = 125.873 - 16.698X + .703X^2 - .009X^3$	17	23.495
	Activity trend evening high density	$Yc = 403.409 - 45.835X + 1.709X^2 - .020X^3$	19	25.123
	Activity trend midnight high density	$Yc = 180.296 - 22.688X + .954X^2 - .012X^3$	21	19.210

Table VIII Factors of weather related to changes in adult activity expressed as percent of daily checks increasing, percent of daily checks decreasing, or percent of daily checks showing no change in counts to spawning beds, Indian River Channel, 1965, 1966.

Year	Period	Bright clear sky or clearing			Dull clouded sky or overcast			Rain			Snow		
		% inc.	% dec.	% n.c.	% inc.	% dec.	% n.c.	% inc.	% dec.	% n.c.	% inc.	% dec.	% n.c.
1965	Daybreak	0.0	50.0	50.0	33.0	55.0	12.0	100.0	0.0	0.0	100.0	0.0	0.0
	Afternoon	0.0	0.0	100.0	50.0	50.0	0.0	100.0	0.0	0.0	50.0	25.0	25.0
	Evening	50.0	50.0	0.0	16.0	84.0	0.0	0.0	0.0	100.0	0.0	100.0	0.0
	Midnight	71.0	15.0	14.0	33.0	67.0	0.0	0.0	100.0	0.0	33.3	33.3	33.3
1966	Daybreak	22.0	33.0	45.0	46.0	36.0	18.0	n.o.	n.o.	n.o.	n.o.	n.o.	n.o.
High	Afternoon	20.0	60.0	20.0	14.0	29.0	57.0	33.3	66.6	0.0	100.0	0.0	0.0
Spawning	Evening	54.0	46.0	0.0	80.0	20.0	0.0	0.0	0.0	100.0	n.o.	n.o.	n.o.
Density	Midnight	36.0	64.0	0.0	50.0	50.0	0.0	100.0	0.0	0.0	n.o.	n.o.	n.o.
1966	Daybreak	11.0	56.0	33.0	45.0	11.0	44.0	n.o.	n.o.	n.o.	n.o.	n.o.	n.o.
Low	Afternoon	20.0	80.0	0.0	42.0	29.0	29.0	67.0	0.0	33.0	0.0	100.0	0.0
Spawning	Evening	46.0	54.0	0.0	80.0	20.0	0.0	0.0	100.0	0.0	n.o.	n.o.	n.o.
Density	Midnight	50.0	50.0	0.0	50.0	50.0	0.0	100.0	0.0	0.0	n.o.	n.o.	n.o.

n.o. = no occurrence